GAS EXCHANGE AND GROWTH RESPONSES OF CITRUS TREES TO PARTIAL IRRIGATION, SOIL WATER, AND ATMOSPHERIC CONDITIONS

By

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By

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Growth and yield of citrus trees in Florida have been reported to be closely related to the portion of rooting zone irrigated, contrary to conclusions of many partial irrigation studies conducted elsewhere. This study was conducted to clarify whole plant gas exchange and growth responses of young citrus trees to partial irrigation of the rooting zone and to investigate the influence of soil water and atmospheric factors on gas exchange through experiments in controlled-environment growth chambers and model simulations of leaf conductance and transpiration.

In an initial study with fully irrigated citrus and three dry-bulb temperature/vapor pressure deficit (DBT/VPD) treatment levels, photosynthetic rates and water-use efficiencies were greatest at the low DBT/VPD (24 °C/1.7 kPa) treatment and remained high when soil water content was low. Increases in DBT and VPD reduced photosynthetic rate and water-use efficiency and resulted in photosynthetic midday depression at the intermediate (29 °C/2.4 kPa) and high (37 °C/3.6 kPa) DBT/VPD levels when soil water content was low.

In a subsequent study, photosynthetic rate and growth of partially irrigated trees on builders' sand declined significantly as the irrigated fraction of rooting volume was reduced 25, 50, and 75 percent. Trees at all levels of irrigation and soil water content experienced severe midday depression of photosynthesis.

In both studies, transpiration increased, but not proportionally, as DBT/VPD increased and was attributed to stomatal closure. At elevated atmospheric carbon dioxide concentrations, midday depression of photosynthesis was observed in the second study, but not in the initial study. The combined findings suggest that midday depression of photosynthesis in citrus results in part from stomatal closure at elevated leaf-to-air humidity deficits, but perhaps more significantly, from increased mesophyll resistance induced by low soil water availability at DBT/VPD levels above 24 °C/1.7 kPa.

Simulated diurnal transpiration rates agreed closely with actual rates of trees with all or 3/4 of their rooting-volume irrigated but declined more rapidly than actual rates in 2/4 or 1/4 irrigated trees. Results of simulations suggest that soil type, evaporative demand, and root-length density are important factors influencing transpiration of fully and partially irrigated citrus trees.

CHAPTER I

INTRODUCTION

Historically, growers have used irrigation with their primary concern being to meet the water requirements of the crop. Increasingly, the focus is shifting towards conserving water so that in some regions the concern of saving water cannot be separated from the concern of providing adequate irrigation for the crop. The development of low-volume or micro-irrigation systems, such as trickle and microsprayers, represents an attempt to satisfy these two, conflicting concerns. Micro-irrigation systems have the advantage over conventional irrigation practices, such as over-head sprinklers or seepage systems, of being able to greatly restrict the soil surface area to which water is applied and thereby reduce water lost by evaporation directly from the soil surface. At the same time, by decreasing the amount of water applied, drainage of water below the root zone is also reduced. Depending on emitter specifications, irrigation frequency and duration, and soil type, water application to the soil surface may wet only a portion of the root system and thus result in what will be referred to here as 'partial rooting volume irrigation,' or simply, 'partial irrigation'.

The dramatic growth in use of micro-irrigation systems for crop production locally and globally justifies the need for an in-depth understanding of crop response to partial irrigation so that low-volume systems may be used in a manner that is both water conservative and nondetrimental to plant growth. Although many studies of partial rooting volume irrigation effects on plant growth, including that of citrus trees, have been performed under a wide range of environmental conditions, this study is unique in that it represents a look at whole plant gas exchange and growth responses of fully and partially irrigated citrus trees in conjunction with soil water and atmospheric temperature/humidity conditions.

An initial study was conducted in sunlit, controlled-environment plant growth chambers to characterize the diurnal rates and patterns of photosynthesis, transpiration, and water-use efficiency of fully irrigated citrus seedlings to both atmospheric and soil water stress. Variation of atmospheric vapor pressure deficit, effected by changes in set-point chamber dry-bulb temperature, and repeated cycles of soil water depletion permitted description of gas exchange responses of citrus seedlings over a wide range of atmospheric and soil water levels as well as identification of conditions conducive to mid-day depression of photosynthesis in citrus. Growth of the citrus seedlings for short periods of time at elevated atmospheric carbon dioxide concentrations was conducted to determine if stress was reduced and if mid-day depression of photosynthesis was alleviated.

In the second part of the study, gas exchange and growth of young, container-grown citrus trees was evaluated as the portion of the root system irrigated was reduced by 75, 50 and 25% that of fully irrigated trees. The objective of this study was to determine if reductions in the irrigated root volume caused reductions in gas exchange rates and growth and if so, what portion of the root volume had to be irrigated to avoid significant reductions in growth as compared to fully irrigated trees. Furthermore, gas exchange responses were assessed not only with respect to the portion of rooting volume irrigated but also with respect to atmospheric evaporative demand and soil water content, i.e., if irrigation of 50% of the root volume was adequate at high water contents and low evaporative demand, did it remain adequate as soil water content was reduced or atmospheric evaporative demand increased?

To manage micro-irrigation systems successfully, knowledge of plant performance with respect to the quantity and distribution of water is needed. But it is also necessary to understand these responses with respect to the major soil, plant, and atmospheric elements and processes determining water availability and use. In the final part of the study, soil, plant, and atmospheric factors were integrated in a model, WATFLW, which describes water movement in the soil and extraction by the plant, the leaf-to-air humidity gradient as the driving force for water movement in the system, and plant regulation of water loss through stomatal conductance. The model predicts leaf conductance and transpiration of fully and partially irrigated citrus trees as influenced by soil type, root-length density, and atmospheric humidity. The model represents an attempt to understand the factors influencing the success of partial rooting volume irrigation practices that will be applicable on a broad scale.

CHAPTER II

REVIEW OF THE LITERATURE

Numerous studies using a variety of plants, including citrus, have substantiated the beneficial effects on plant growth and crop yield of supplemental water application during periods of soil water stress (Huberty and Richards, 1954; Beutel, 1964; Hilgeman and Sharp, 1970; Shmueli et al., 1973; Levy et al., 1978). But because fresh water resources for irrigation purposes are not available in unlimited quantities, a better understanding of water use by plants is sought. An extensive array of sophisticated irrigation technology including piping, pumping equipment, emitters, filters, valves, and computerized control systems already exists to supply water to plants. Yet, lagging behind the knowledge of designing and controlling irrigation systems is an integrated understanding of water availability to crops and plant response to the timing, frequency, and quantity of irrigation. It is undoubtedly from these areas that the next significant advances in irrigation water use efficiency will proceed. The following discussion reviews and integrates work in the area of citrus irrigation and response to soil and atmospheric moisture stress with that concerning water movement in the soil-plant-atmosphere system.

Citrus Irrigation in Florida

The need to irrigate citrus in Florida arises from three main environmental constraints: (a) uneven seasonal rainfall distribution, (b) the low water holding capacity of soils on which citrus is grown, and (c) shallow, seasonally fluctuating water tables which restrict rooting depth and hence the volume of soil available for rooting zone water storage for about half of the citrus acreage (Allen et al., 1982; Rogers et al., 1983). Most rainfall occurs during the months of June through October, whereas rainfall from March through May may be less than that required for citrus growth. This period of deficit precipitation coincides with critical times of new growth, flowering, and fruit set in citrus. At the same time, the useable water storage capacity, defined as 70% of the available water storage, of soils in Florida on which citrus is grown ranges from 0.8 to 11 cm per meter (Reitz et al., 1981). Thus, soil water reserves are often limited and must be replenished frequently.

Early irrigation studies of citrus in Florida established its beneficial effects on plant growth and fruit production and also formulated guidelines for the timing and amount of water application (Koo and Sites, 1955; Koo, 1963; Koo 1969; Koo and Hurner, 1969; Koo et al., 1974; Harrison and Koo, 1973). Traditional methods of citrus irrigation in Florida, such as permanent overhead sprinklers, furrow seepage, and crown flood irrigation, use large volumes of water. Furthermore, just as much water may be applied during the seedling stage as to larger trees (Rogers et al., 1983). It is estimated that irrigation of agricultural crops in Florida constitutes 41% of Florida's consumption of extracted fresh water and irrigation of citrus alone comprises the largest fraction of irrigated acreage in the state (Harrison et al., 1983).

Demand for Florida's fresh water resources has been a growing conflict between urban, industrial, and agricultural interests over the years. In 1972 the Florida legislature passed the statewide Water Resources Act which declared all waters of the state subject to regulation. Five water management districts were formed and given authority to grant legal permits which are required for physical modifications affecting water flow, quality or storage and the consumptive use of water (Baldwin and Carriker, 1985). The permitting system is the main regulatory tool used by the agency to monitor the consumptive use of water. Historically, water allocations to growers were determined on the basis of the amount of water used by the grower in the past. But, as the demand of Florida's urban population for fresh water increases, it is inevitable that water allocations for irrigation purposes will be reduced. This is especially true in those districts, primarily located in southern Florida, with densely populated urban areas and intensive agricultural activity. Increasingly, water allocations for irrigation purposes are being determined on the basis of the estimated water requirements of the crop and water usage of efficient, water conservative, low-volume irrigation systems. Consumptive use permits carry expiration dates and already some water management districts are reducing water allocations for irrigation by as much as 70% at the time permits are renewed (Bateman, 1987).

Low-Volume Irrigation of Citrus

Low-volume irrigation systems, which include drip, trickle, and microsprinkler systems, apply reduced volumes of water at low pressures to a limited area of soil. Since introduction of low-volume systems in Florida in 1971 their use has grown steadily (Harrison and Zazueta, 1984). Nearly all new citrus plantings in the southern portion of the state in recent years have been established with low-volume irrigation systems (Fisher, 1984; Hardy, 1985).

The ability of low-volume systems to improve water-use efficiency lies in the fact that it is possible to apply a reduced amount of water directly to the soil volume where roots are concentrated, thereby reducing water lost by evaporation from the soil surface or percolation below the root zone. High water content levels are maintained in the wetted zone of soil in order to meet transpiration demands of the shoot. Although this characteristic of reduced soil volume wetting is considered advantageous in terms of water conservation, it has stimulated concern over the possible detrimental effects on crop growth resulting from incomplete irrigation of the root system.

Water movement in the soil under low-volume systems is three-dimensional, as compared to one-dimensional movement under conventional systems where the entire surface area is wetted (Brandt et al., 1971). Incomplete, or partial, irrigation of the root zone, and thus root system, can occur when water applied to a limited surface area moves predominately vertically in the soil in response to gravitational forces, with consequent limited lateral movement. The actual distribution of water in the soil is determined by the emitter type and placement, the rate, duration, and frequency of water delivery, and the soil texture. Limited lateral movement of water is generally a problem in coarse-grained, sandy soils. In Florida, the soil water content at 30 to 76 cm depths was determined to be less than adequate for plant availability at distances of 15 to 46 cm from emitters on well-drained soils and 15 to 152 cm on poorly drained soils (Koo and Tucker, 1974). Water availability on poorly drained soils generally was adequate up to 152 cm from emitters below a depth of 30 cm primarily due to upward movement of water from high water tables. The maximum diameter of the wetted area under emitters with a discharge rate of 4 liters per hour on Florida soils ranged from 0.6 to 1.5 m, depending on the soil texture. This may represent 2 to 15% of the soil in the root zone, depending on tree spacing. Myers and Harrison (1978) estimated that, on sandy soils in Florida, 3 or 4 emitters per tree would be expected to wet 12 to 16% of the soil volume allocated to a mature tree whereas, on soils with finer texture, 40 to 60% might be covered with the same emitter density. Because of the narrow distribution of water in the soil, root development under low-volume irrigation systems is frequently confined to a smaller soil volume than for sprinkler irrigated trees. Plant stress may be incurred more frequently and more rapidly in plants irrigated with low-volume systems due to rapid depletion of water in the wetted region of soil. Thus, trees that experience seasonal growth of roots outside the irrigated soil volume, or trees that are in groves converted to low-volume irrigation systems, may not be able to transport sufficient water to the shoot due to the reduced amount of active roots.

Early concern over partial irrigation of the root system of tree crops arose when it was suggested that the water-use efficiency of flood or furrow seepage systems could be improved if alternate sides of the tree row were irrigated on successive dates. Furr and Taylor (1939) investigated the problem by severing various portions of roots of mature citrus trees and measuring fruit volume change on subsequent dates as an indication of the ability of the reduced root system to supply adequate water to the shoot. They concluded that lemon trees could obtain adequate water when less than 100% of their root system was wetted by alternate row irrigation. The practice of alternate row irrigation became a recommended practice for citrus (Johnston, 1949). Several other early studies in California (Huberty and Richards, 1954) and in Arizona (Hilgeman, 1970) contributed results supporting the beneficial effects of alternate row irrigation of citrus. In Israel, several studies conducted in the 1960's showed that alternate row irrigation increased yields while reducing water use (Shmuelei et al., 1973). But, an early study of alternate row irrigation of citrus trees in Australia showed significant reductions in the butt circumference and yield of trees irrigated on one side as compared to trees irrigated on both sides. The authors concluded that this method of water application was not adequate to supply the water demands of the tree (Bouma and McIntyre, 1963).

Numerous studies since this early interest have been conducted with citrus, as well as other fruit tree species, to assess the relative success and efficiency of low-volume and traditional irrigation methods. In general, relative root volumes irrigated were not estimated or measured in these studies. Comparable, or improved, performance of citrus irrigated with low-volume systems as compared to those irrigated with traditional systems were reported in California on a clay loam (Aljibury et al., 1974), in Arizona on a sandy soil (Rodney et al., 1977), and in Arizona on a sandy soil underlain with silt (Roth et al., 1981). But, superior performance of sprinkler irrigated trees compared to drip irrigated trees has been reported for citrus as well as other tree crops. In Australia citrus trees on deep, sandy soils showed superior yields under sprinkler irrigation as compared to drip irrigation. Low yield from the drip treatments was attributed to leaching of nutrients in the root zone due to excessive water application (Cole and Till, 1974). In Israel, Bielorai (1985) reported that grapefruit with two drip lines yielded more than trees with a single drip line. The beneficial effect was attributed to an increase in the surface area irrigated. Proebsting et al. (1984) found that trickle-irrigated apple trees experienced greater water stress and had less vegetative growth than sprinkler irrigated trees.

Apart from a study by Myers and Harrison in 1978, results of low-volume irrigation studies of citrus in Florida have not indicated the degree of success that has been achieved in other locations. In an early study of drip irrigated citrus, Koo and Tucker (1974) concluded that irrigating 60% of the soil in the root zone was adequate to maintain high fruit production. However, their recommendation appears to have been based in part on results of a separate, previous study with sprinkler irrigated trees which indicated that the greatest increase in fruit production was obtained when soil water in the root zone was maintained at 60 to 65% of the field capacity value. Thus, it appears that the authors concluded that irrigating 60% of the root-zone was comparable to maintaining the entire root zone at 60% of the field capacity. This assumption does not appear to have been adequately tested.

In a later study on Astatula fine sand in Florida, tree growth and fruit yield were compared for nonirrigated citrus trees and trees irrigated with low-volume systems that wet 15 to 25, 30 to 40, or 70 to 78% of the under canopy soil surface area (Koo, 1978). Greatest tree growth was obtained with irrigation that wet 70 to 80% of the soil area and fruit production was reported to vary directly with the ground area irrigated. It was concluded that the greater the grove floor area irrigated, the higher the fruit yield but, because these results were obtained on a high density planting, this recommendation was not endorsed for standard density plantings. A subsequent investigation on a standard density grapefruit planting on Astatula fine sand showed that tree growth was affected more by the ground surface area wetted than by the rate of water application. Fruit production increases over the no irrigation control were 8% for drip, 20% for jet, and 72% for sprinkler irrigation. It was concluded that irrigation coverage was the most important factor affecting tree growth and fruit yield, and it was recommended that irrigation systems be designed to cover as much ground surface area as possible (Koo, 1985a). Other studies conducted in Florida reiterate these findings and recommendations (Koo, 1984; Koo and Smajstrla, 1985; Smajstrla and Koo, 1985; Zekri and Parsons, 1988, 1989).

Results of partial root-zone irrigation studies in Israel have generally been more positive, though more variable, than results obtained in Florida. Typically, studies in Israel were conducted on sandy clay loams or heavy clays with greater water holding capacities than soils in the Florida studies. In an eight-year comparative study of drip and sprinkler irrigated Marsh grapefruit, no differences in yield due to the irrigation system used were reported (Yagev and Horesh, 1981). In a separate study, drip and sprinkler irrigation were used on a loam soil to compare the effect of wetting 30, 40, or 70% of the root zone using a range of irrigation frequencies. During the first three years of the study, drip irrigation that wet 30 or 40% of the root zone of mature citrus trees produced lower yields than sprinkler irrigated trees with 70% of their root zone irrigated. By the fourth year, yields of the drip irrigated trees were equal to, or greater than, yields of the sprinkler irrigated trees (Bielorai, 1977). Several other studies of similar nature conducted in Israel reported acceptable performance of drip irrigated trees compared to sprinkler irrigated trees (Bielorai et al., 1981; Bielorai, 1982; Bielorai et al., 1984). Moreshet et al. (1983) reported that citrus trees in Israel with 40% of their root zone irrigated had reduced transpiration rates and exhibited greater water stress, as indicated by lower predawn and noontime leaf water potentials, than trees with fully irrigated root zones. Yields did not differ between treatments during the first year but were reduced in the partially irrigated treatment during the second year. Cohen et al. (1987) also reported water stress in partially irrigated citrus and attributed it to decreased hydraulic conductance of the tree resulting from decreased water transport in the portion of roots occupying the nonirrigated regions of soil.

A major difficulty in assessing the effect of partial root-zone irrigation of mature trees in the field lies in defining the root-zone or soil dimension used to quantify the irrigation treatment. Several different root-zone parameters have been used for partial irrigation studies: percentage soil surface area (Bielorai, 1982), root-zone soil volume (Bielorai et al., 1981; Bielorai 1977), relative soil volume per tree (Moreshet et al., 1983), under tree canopy area (Koo, 1978; Smajstrla, 1985; Koo, 1985b). Use of such dimensions makes it difficult to compare results of different studies or relate results to the actual volume or portion of roots receiving water. An improvement over these descriptions of root zone dimensions is possible with use of split-root techniques. Typically, the procedure involves pruning the taproot or actually dividing it vertically into separate portions and establishing plants with separate, nearly equal, root volumes upon which treatments may be applied. The technique has been used for a variety of horticultural crops including citrus (Koch and Johnson, 1984; Zekri, 1984). Evidence of transverse flow of water in the vascular system of citrus validates use of this technique for studying varying levels of edaphic treatments on the entire shoot. Dye injected into the stem of citrus trees left traces in all branches present (De Villiers, 1939). Similar findings were reported in Sitka spruce (Coutts and Philipson, 1976).

Division of the root system into four separate portions to study the effect of partial root volume irrigation has been performed on several crops. In a study in Australia, apple trees (Malus domestica) with 4-part split roots were established with each root mass growing in a separate container. One, two, three, or all of the containers were irrigated to simulate wetting 25, 50, 75, or 100% of the entire root volume, respectively. Water lost through transpiration, expressed as percentage of the fully irrigated treatment, was 74, 88, and 94% for the 25, 50, and 75% irrigated treatments, respectively. It was concluded that wetting substantially less than the entire root system at frequent intervals would be comparable to wetting the entire root volume less frequently (Black and West, 1974). In a separate study utilizing the same technique it was concluded that apple root systems had the ability to increase their rate of both water and nitrate-nitrogen uptake so that about 2/3 of the root system could provide adequate water and nitrogen (Frith and Nichols, 1974). Four-part split-root peach (Prunus persica) seedlings grown in containers with separate compartments exhibited only small reductions in transpiration and negligible reductions in photosynthesis, stomatal conductance, and xylem pressure potential of partially irrigated plants as compared to the fully irrigated plants. Both stem and leaf dry weight accumulation were described as linearly related to the fraction of root system irrigated. It was concluded that 50% of the root system was able to provide adequate water to the plant when the wetted soil was maintained near field capacity (Tan and Buttery, 1982). In similar study the response of tomato (Lysopersicon esculentum) plants to partial root zone irrigation indicated no simple linear relationship between the fraction of root system supplied with water and transpiration rate. It was found that restricting water application to 50% of the root system did not cause a reduction in transpiration, photosynthesis, or stomatal conductance. It was proposed that the absorption capacity of tomato roots was increased in response to transpiration demand (Tan et al., 1981).

Although synthesis of results from the above cited studies is difficult due to differences in soil types, plant specifications, water application, and evaporative demand, it is apparent that water placement in the soil, as determined by the location, area and depth of wetting, and the duration and frequency of water application, are key factors which can be manipulated to increase water availability for tree crops irrigated with low-volume systems. Two other factors that strongly affect water availability, but cannot be controlled by the grower, are the water holding capacity of the soil and the atmospheric evaporative demand.

Soil Water Availability

The availability of water for transpiration has been the subject of studies as early as 1912. Brown (1912) described the problem in an intuitive sort of way:

> Since transpiration is due to the ability of the air to remove water from the leaves, the soil moisture content at which wilting occurs should depend on the evaporating power of the air (Brown 1912, p. 121).

It was the belief of Brown and others that plants experience stress as the water content of the soil decreases and that the climatic conditions experienced by the plant have an important influence on the level of soil water at which permanent wilting is experienced. Proponents of the contrasting view held that soil water is equally available to plants within the range of field capacity to permanent wilting and that the water content at permanent wilting is a characteristic of the soil and is relatively unaffected by the plant growing thereon or the climatic conditions to which it is exposed.

The question of soil water availability for transpiration resurfaced in the 1950's and 60's. In 1950 Veihmeyer and Hendrickson reviewed many studies which supported the concept of unlimited water availability until the permanent wilting point was approached. In 1957 Stanhill reviewed 80 papers on the subject of soil water availability. He concluded that the results of 66 of these papers showed that plant growth was affected by the degree of depletion of available soil water and that atmospheric evaporative conditions needed further consideration. Subsequently, Denmead and Shaw (1962) reported that the actual transpiration rate of corn fell below potential transpiration as the soil water was depleted and that the soil water content at which transpiration began to decline occurred at higher soil water contents as the potential transpiration rate increased. Soil water availability for transpiration in citrus specifically has not received much attention. Reed and Bartholomew (1930) reported that the damaging effects of desiccating winds on citrus trees growing on Ramona gravelly loam was influenced by soil structure and root distribution. Lombard et al. (1965) concluded that the most important factor influencing leaf water deficit of navel orange trees on Ramona sandy loam was soil water movement when soil water potential was less than -.02 MPa. It is apparent that the question of soil water availability for transpiration does not possess a single answer but that the soil, plant, and atmospheric conditions in any particular case must be considered.

Consideration of water availability and application of the concept of water movement in the soil-plant-atmosphere continuum is appropriate to a study of partial root volume irrigation of citrus in Florida due to extreme edaphic and atmospheric conditions that may be encountered as well as certain physiological characteristics of citrus. Understanding the soil, plant, and atmospheric conditions that influence water movement and determine water availability may provide a sound basis for determining the relative advantages or disadvantages of partial root volume irrigation and will be useful in decisions regarding irrigation timing and quantity. The following section reviews some pertinent concepts of water movement in the soil-plant-atmosphere continuum (SPAC) and in brief discusses some existing models of water movement in the SPAC.

The Soil-Plant-Atmosphere Continuum

The lack of a comprehensive theoretical treatment of soil water movement was likely responsible in part for conflicting results that were reported from early studies of soil water availability. Philip (1957) and Gardner (1960) contributed much to quantitative treatment of the problem by analyzing the rate of soil water movement to the plant root. Subsequently, application of the concept of water movement in the soil, plant, and atmosphere as a catenary process determining water availability for transpiration was utilized by a number of workers and provided the outline for improved quantitative assessment of the problem.

Water movement through the SPAC has been described using various forms of the general transport equation:

$$\text{Flux} = \frac{\text{driving force}}{\text{resistance}} \tag{2.1}$$

Gradmann (1928) introduced the concept of an electrical resistance analog based on Ohm's Law to describe water movement through the SPAC. The concept was further developed by Van den Honert in 1948 but was not popularized until the 1960's. Steady-state flow of water in the SPAC is described by:

$$\text{Flux} = \frac{\psi_s - \psi_{rs}}{r_s} = \frac{\psi_{rs} - \psi_x}{r_r} = \frac{\psi_x - \psi l}{r_x + r_l} = \frac{\psi_l - \psi_a}{r_a} \tag{2.2}$$

where,

Flux = volume flux density, $m^3\ m^{-2}\ s^{-1}$,

$\psi_{s,\,rs,\,x,\,l,\,a}$ = the chemical potential of water in the soil, root, xylem, leaf and air, respectively, MPa,

$r_{s,\,r,\,x,\,l,\,a}$ = resistances in the soil, root, xylem, leaf and air, respectively, MPa s m^{-1}.

The concept of water potential is frequently employed in the study of plant water relations to describe the partial molal Gibbs free energy of water under specific conditions. The equation describing water potential is derived from the chemical potential of water:

$$\mu_w = \mu_w^* - V_w\pi + V_wP + m_wgh \qquad (2.3)$$

where,

μ_w = the chemical potential of water of the system under consideration, in units of energy per mole of water, e.g., J mol^{-1},

μ_w^* = the chemical potential of water under standard state conditions, being pure water at atmospheric pressure and at the temperature and altitude of the system under consideration, J mol^{-1},

V_w = the partial molal volume of water, m^3 mol^{-1}

P = hydrostatic pressure, MPa,

π = osmotic pressure, MPa,

m_w = mass per mole of water, kg mol^{-1},

g = gravitational acceleration, m s^{-2},

h = height above reference point, m.

The difference in chemical potential between water under standard conditions and under conditions of the system concerned, (μ_w - μ_w^*), represents the ability of water in the system to do work. A difference in this term between two regions indicates nonequilibrium and consequently water will tend to move towards regions of lower potential, ψ, described by Nobel (1983) as

$$\psi = \frac{\mu_w - \mu_w^*}{V_w} = P - \pi + \rho_wgh \qquad (2.4)$$

where ρ_w equals m_w/V_w.

Except when considering water potential gradients in tall trees, the gravitational potential term is disregarded and water potential is defined as

$$\psi_l = \psi_p + \psi_\pi \tag{2.5}$$

where

ψ_l = total potential of, in this case, the leaf, MPa,

ψ_p = pressure potential, MPa,

ψ_π = osmotic potential, MPa.

The electrical resistance analogy describes water flux as proportional to the water potential difference between two regions of the system and inversely proportional to the resistance in that region. Although application of the Ohm's Law analog to the problem of water movement in the soil-plant-atmosphere system is not entirely valid due to assumptions of isothermal conditions and independent flow of water and solutes as well as phase changes involved (Cowan, 1965), it is widely used because it elucidates driving forces and resistance factors throughout the system.

The Soil

Soil water potential is defined as

$$\psi_s = \psi_p + \psi_\pi + \psi_m + \psi_g \tag{2.6}$$

where

ψ_s = total water potential of the soil,

ψ_p = pressure potential,

ψ_π = osmotic potential of soil solution,

ψ_m = matric potential,

ψ_g = gravitational potential.

Pressure potential is negligible, except in cases of ponded or saturated soil. The osmotic potential of soil solution may also be considered negligible in influencing water movement over relatively large distances so that the total potential of soil water is largely determined by the matric forces and its position with respect to some reference point.

Steady-state, one-dimensional flow of water in saturated soil was first described by Darcy (1856) and has since been referred to as Darcy's Law

$$Q = -K\left(\frac{\partial\psi}{\partial z}\right) \tag{2.7}$$

where

Q = volume of water per unit cross-sectional area per unit time,

K = hydraulic conductivity of the soil,

ψ = total soil water potential,

z = distance in the direction of flow.

Slichter (1899) rewrote Darcy's Law to describe transient flow in three dimensions

$$Q = -K\left(\frac{\partial\psi}{\partial x} + \frac{\partial\psi}{\partial y} + \frac{\partial\psi}{\partial z}\right) \tag{2.8}$$

where x, y, and z represent distance along the respective orthogonal axes. Richards (1931) applied Darcy's Law to water movement in unsaturated soils with the provision that hydraulic conductivity be dependent on the soil matric potential:

$$Q = -K(\psi)\left(\frac{\partial\psi}{\partial x} + \frac{\partial\psi}{\partial y} + \frac{\partial\psi}{\partial z}\right) \tag{2.9}$$

To obtain the general equation of flow, it is necessary to introduce the continuity equation which states that change in the flow velocity through a volume of soil is equivalent to the volume rate of change of water in that volume:

$$\frac{\partial \theta}{\partial t} = -\nabla \cdot Q \tag{2.10}$$

where

θ = volumetric water content,

∇ = differential operator.

By combining the continuity equation with Richards' equation, the transient, three-dimensional, unsaturated flow of soil water can be described as

$$\frac{\partial \theta}{\partial t} = \nabla \cdot [K(\psi)\ \nabla \psi\ ] \tag{2.11}$$

As the soil dries, the film of water surrounding the soil particles shrinks and resistance to water movement increases as the size of the soil pores through which water is able to move decreases. The amount of water in the soil at equilibrium is a function of the size and volume of the water-filled pores and hence a function of the matric suction potential. The volumetric water content to matric potential relation is measured experimentally and depicted by soil-water retention curves. The soil-water retention curve is largely determined by soil texture. In sandy soils most pores are relatively large and release their water at low matric potential so that compared to a clayey soil, which has smaller pores, the water content at any given soil water potential (except near saturation) will be lower. The hydraulic conductivity, which represents the slope of the flux versus the driving force or hydraulic head gradient, is also highly dependent upon the soil porosity and pore size. Similar to the volumetric water content-soil water potential relationship, the unsaturated hydraulic conductivity in sandy soils decreases more rapidly with increasing suction than in clayey, or fine-grained soils (Hillel, 1982).

Soils on which citrus is grown in Florida tend to be coarse grained with low water holding capacities and low unsaturated hydraulic conductivities. The citrus growing regions of Florida are often categorized according to their topography with two major types of planting sites recognized: the Central Florida Ridge and the Southern Florida Flatwoods (Caldwell, 1980). Ridge sites are located in a region, about 50 miles wide, that extends from the north central part of Florida southward for approximately 200 miles. This region of rolling hills and lakes has been referred to as the 'Citrus Ridge'. Soils in this region, classified mainly as Entisols, typically have water holding capacities at field capacity of 6 to 8%, and low unsaturated hydraulic conductivities. Flatwoods sites are not confined to a certain region but are characterized by flat lands with poor drainage and variable soils. The Spodosols on these sites have a sandy layer with low water holding capacity underlain by a layer with reduced permeability.

The water supplying capacity of soils on Ridge and Flatwoods sites is also significantly determined by the soil volume available for root growth. On Ridge sites the deep, well-drained sands permit extensive exploration of the soil. Roots have been found at depths of 2.1 to 3.7 m

(Castle and Krezdorn, 1975) and feeder roots may extend to depths of 1.54 m or more (Tucker, 1980). On Flatwoods sites shallow water tables can exist above the layer of low permeability during periods of abundant rainfall or excessive irrigation and cause flooding of the root-zone. Citrus grown on these sites must be planted on raised beds to provide an unsaturated soil volume for root growth. The variable depth of ground water tables on Flatwoods sites often restricts root development to the upper 0.45 m of soil (Calvert et al., 1981; Obreza and Admire, 1985; Graser and Allen, 1987). The combination of these factors--low water content, low hydraulic conductivity and, in many locations, low rooting volume--can result in severely restricted water reserves for plant growth on most Florida soils.

Uptake of soil water by the root system has been described variously using approaches that have been categorized as either the single root model or the root system model (Molz and Remson, 1970). The single root model, or 'microscopic' approach, considers the radial flow of water to an individual root which is described as an infinitely long cylinder of uniform radius and water absorbing properties. This approach has been employed by Philip (1957), Gardner (1960), Cowan (1965), Passioura and Cowan (1968), Molz and Remson (1970), Whisler et al., (1970) and Hillel et al., (1975). The root system model or 'macroscopic' approach disregards flow towards individual roots and utilizes an extraction term as a function of a number of factors such as time, space, moisture content, and transpiration rate, to describe the water uptake from each differential volume of the root system. The disadvantage of this approach is that it does not consider differences in soil water potential between the bulk soil and the immediate vicinity of the roots. Models of this type have been employed by Ogata et al. (1960), Gardner (1964), Molz and Remson (1970, 1971), Nimah and Hanks (1973), and Hillel et al. (1976). Slack et al. (1977) combined the single root and root system model to predict water uptake patterns. The single root model is discussed below and a brief discussion of the root system model is presented in a later section.

The single root model expresses the general flow equation in radial coordinates and for transient radial flow can be written:

$$\frac{\partial\theta}{\partial t} = \frac{1}{r}\frac{\partial}{\partial r}\left(rK(\psi)\frac{\partial\psi}{\partial r}\right) \qquad (2.12)$$

or

$$\frac{\partial\theta}{\partial t} = \frac{1}{r}\frac{\partial}{\partial r}\left(rD\frac{\partial\theta}{\partial r}\right) \qquad (2.13)$$

where

r = the radial coordinate,

D = soil water diffusivity.

As an approximation of the transient flow equation Gardner (1960) proposed use of the steady-state solution for flow in a hollow cylinder. The difference between the soil matric potential at the root-soil interface and some distance from the root could then be calculated as:

$$\psi_a - \psi_b = \frac{q}{4\pi K}\ln(r_b^2/r_a^2) \qquad (2.14)$$

where

ψ_a = matric potential at the surface of the root,

ψ_b = matric potential at the outer radius of the cylinder of soil surrounding the root,

q = steady-state rate of water uptake per unit length of root,

r_a = radius of the root,

r_b = radius of the cylinder of soil surrounding the root, calculated as $1/\pi L$, where L is the root-length density, cm cm^{-3}.

Philip's analysis (1957) showed that the water content at which a plant undergoes stress depends on the transpiration rate, the extent of the root system, the soil water diffusivity, and the characteristic plant water potential at which wilting symptoms appear. Gardner (1960) showed that at lower matric potentials water movement can be a limiting factor to water availability. The soil-water content at which the hydraulic conductivity of the soil becomes a problem depends upon the rate of water uptake per unit length of root (q), and therefore will be sensitive to estimates of the extent of the root system.

Newman (1969), however, argued that unrealistically low values of rooting density and high values of water uptake rates used by Gardner and Cowan resulted in incorrect estimates of rhizosphere resistance. Newman was joined by others who also argued that, in reality, rooting densities are so high and the rate of water uptake per length of root so low that it is only when soil matric potential falls below -1.5 MPa that the rate of water movement to the root becomes limiting (Lawlor, 1972; Hansen, 1974; Taylor and Klepper, 1975). Carbon (1973), using predictions of water flow to roots obtained from an alternate model proposed by Whisler et al. (1970), proposed that low rates of water supply to roots could indeed be a problem on coarse soils when the matric potential was less than -0.1 MPa. Both theoretical and experimental results with sorghum indicated that a significant rhizosphere resistance existed due to inability of the soil to transport water at rates sufficient to prevent rapid decline in plant water potential during the day. Plant water stress resulted in reduced growth and yield.

Hillel et al. (1975) employed the single root model to evaluate gradients in soil moisture potential in the vicinity of the roots and the magnitude of error resulting from use of the root system model. Their results showed that the plant water potential required to maintain water extraction at the full rate of atmospheric evaporative demand decreased more (more negative) when localized depletion of water in the root vicinity was considered than when soil moisture depletion was assumed to be uniform throughout the soil. Soil water potential gradients were much steeper in the vicinities of roots in the case of low root densities than high root densities as well as for high evaporative demand. They concluded that the effects of localized depletion of water in the vicinities of roots can be important, particularly for young plants growing in soils with low water holding capacities and low unsaturated hydraulic conductivities.

While early studies of the SPAC placed the major resistance to water flow in the soil, there has certainly been much disagreement on this point. Other work indicated that the major resistance to water flow into plants was at the soil-root interface and resulted from root shrinkage and decreased root to soil contact as the soil dried

(Herkelrath et al., 1977a,b; Faiz and Weatherly, 1978; Huck et al., 1970). Still other workers reported that root resistance exceeds that of the soil and constitutes the major control factor for water movement into roots (Taylor and Klepper, 1975; Reicosky and Ritchie, 1976; Blizzard and Boyer, 1980).

Passioura (1982) concluded that while there is little doubt that matric potential gradients in the rhizosphere are important in dry soils, clarification of their importance in moist soils is hindered by the lack of adequate measurements of the soil hydraulic properties by many workers as well as the lack of reliable estimates of the proportion of the total root length effective in absorbing water.

The Root

The rate at which water is taken up by roots is determined not only by the rate at which the soil can transport water to the root surface but also by the hydraulic conductivity of the roots and the total absorbing area of the root. The path of water movement into the root is believed to be along the cell walls of root hairs and across the cortical tissue via the free space up to the suberized Casparian strip on the radial and horizontal walls of the endodermis. From there water is forced through the symplasm of the endodermis and subsequently into the xylem (Greacen, 1977). Flow of water into the root is controlled largely by the resistance to radial flow at the endodermis with comparatively negligible resistance in the axial path (Taylor and Klepper, 1975).

Measurements of citrus root hydraulic conductivity have been used largely as a tool in comparative studies of water transport efficiencies of different rootstocks (Syvertsen, 1981; Syvertsen and Graham, 1985) or in response to edaphic stresses (Ramos and Kaufmann, 1979; Wilcox and Davies, 1981; Syvertsen and Smith, 1983; Levy and Syvertsen, 1983; Graham and Syvertsen, 1984; Syvertsen et al., 1983). In general, hydraulic conductivity declined with decreased soil temperature or soil drying and in the case of water stress was attributed to increased suberization of roots. Castel (1978) partitioned the total hydraulic resistance of rooted Valencia cuttings between leaves, stems, and roots and obtained ratios of approximately 1:1.3:4.1. Although these studies provide estimates of the magnitude of hydraulic resistance in the citrus root system, there are no reports of the relative importance of root hydraulic resistance to water transport throughout the SPAC.

Relatively few estimates of the extent of the citrus root system are available. Wallace and Nauriyai (1958) estimated the total root length of an orange tree to be 10 to 29 miles long which they state is less extensive than that of a wheat plant. Kriedemann and Barrs (1981) described the citrus root system as sparse while Zekri (1984) described it as 'dense'. Neither gave values of root length density (RLD). Values of RLD of citrus from other sources range from very low, 0.23 to 0.52 cm of root length per cm^{-3} of soil volume (Mikhail and El-Zeftawi, 1980) to average for fruit trees, 1.5 to 1.3 cm cm^{-3} (calculated from Bevington and Castle, 1982). Marler (1987) reported a RLD of 0.5 mm dm^{-3} for young nonirrigated trees at a distance of 80 cm from the trunk and 9.8 mm dm^{-3} for irrigated trees at 40 cm from the trunk. Conversion to cm cm^{-3}

results in extremely low values of 0.5×10^{-4} and 9.8×10^{-4} cm cm^{-3}. These values were obtained by calculating RLD from root concentration (number of roots per area of soil) values. While it is recognized that RLD values of trees are typically lower than those of herbaceous crops, it is uncertain whether the RLD of citrus may be a limitation to water transport in the SPAC and therefore merits further attention.

The concept of water movement in the SPAC has been used by a number of workers to interpret plant water relations measurements in citrus (Elving et al., 1972; Kaufmann and Hall, 1974; Camacho-B et al., 1974a,b; Kaufmann, 1977). Changes in leaf water potential with increasing water flux and variable resistances were studied using the following model

$$\psi_{leaf} = \psi_{soil} - (\text{flux})\cdot(r_{\text{soil to leaf}}) \qquad (2.15)$$

Deviations from the nonlimiting leaf water potential to water flux relationship when edaphic stresses of water deficit and low temperatures were imposed were attributed to changes in the resistance term. It was proposed that the nonlimiting leaf water potential-water flux relationship provided a stable relationship for evaluating leaf water potential measurements. Although component resistances in the soil-to-leaf portion of the system were not measured, several of the studies suggested that the major resistance was located in the roots. One study estimated water flow in citrus stems using the heat pulse technique and concluded that decreased water uptake was the result of reduced transport of water in the soil towards roots (Cohen et al., 1983).

The Stem

Resistance to water movement through the stem is generally considered to be negligible compared to resistances that may be encountered in the soil and root portion of the system. But, work by Turner et al. (1984) with several woody and herbaceous species indicated that water transport in the stem of the woody species may be important in determining leaf water status. De Villiers (1939) provided comparative estimates of water transport in the stem of three citrus species. Water conductivity in the xylem was greatest for rough lemon and least for sour orange. The low conductivity of sour orange was attributed to small xylem vessel diameter, short vessel-segments and the small number of vessels. Xylem anatomy studies were performed on stem segments only. Estimates of water flow in citrus stems derived from heat pulse velocities also suggest high resistance to water flow in sour orange stems (Gale and Poljakoff-Mayber, 1964).

The Leaf

The water vapor density difference between the leaf and the atmosphere provides the driving force for water movement through the soil-plant-atmosphere continuum. It is also in the leaf that the greatest resistance to water flow in the system is encountered. Water evaporating from mesophyll cell surfaces within the leaf travels throughout the intercellular airspaces and exists the leaf via stomata. Measurements of stomatal resistance represent the sum of series resistances to evaporation and water vapor diffusion encountered at the surface of the mesophyll cell wall, in the intercellular air spaces, at the stomatal opening and across the boundary layer at the leaf surface, although the latter represents a nearly constant, negligible factor in measurements made with steady-state diffusion porometers. Stomatal movement depends on turgor regulation in the epidermis. It is generally assumed that environmental stimuli are perceived by guard cells and transduced into controlled ion fluxes resulting in concomitant changes in water content and turgor (Zeiger, 1983). Increases in turgor generate mechanical forces on the thickened walls of the guard cells resulting in stomatal opening. This response has been well documented for stomatal response to light (Shimazaki et al., 1986) and a similar mechanism has been suggested for stomatal response to leaf-to-air humidity deficits (Grantz and Zeiger, 1986).

Minimum values of leaf resistance for citrus greater than 1.0 s cm^{-1} are commonly reported, whereas values for some herbaceous crops are typically less than 1 s cm^{-1}. Table 2.1 gives examples of reported values of leaf resistance for several crop species. Observed ranges in leaf resistance reported for citrus are shown in Table 2.2; environmental conditions under which the values were obtained varied and include both water stress and non-stress conditions. The reader is referred to the citations for the specific conditions of each study. Response of citrus leaf resistance to environmental and physiological conditions has been described for radiation (Kriedemann, 1971; Hall et al., 1975b; Vu et al., 1986), temperature (Hall et al., 1975; Khairi and Hall, 1975a), plant water status (Halevy, 1956; Hilgeman et al., 1969; Kaufmann and Levy, 1976; Levy, 1980; Meyer and Green, 1981; Syvertsen et al., 1981; Syvertsen, 1982; Zekri and Parsons, 1988), and leaf-to-air humidity

Table 2.1 Leaf resistance for several crop species.

r_l, s cm^{-1}	Crop
0.38 - 0.54	Sunflower
0.24	Tobacco
0.41	Corn
0.25 - 2.4	Wheat
1.60	Sugar beet
1.6 - 1.8	Cotton
1.6 - 1.8	Sorghum
1.0 - 2.0	Peanut
1.0 - 2.0	Soybean
2.4 - 3.4	Tomato

From: Mantell, 1977

Table 2.2. Reported ranges of citrus leaf resistance

r_l, s cm^{-1}	Source
1 to 10	Hilgeman et al., 1969
5 to 15	Allen and Cohen, 1974
1 to 5	Hall et al., 1975
7 to 20	Kaufmann and Levy, 1976
8 to 20	Levy, 1980
<1 to 2	Levy and Syvertsen, 1981
<1 to 1	Meyer and Green, 1981
0.5 to 20	Syvertsen et al., 1981
10, mean	Syvertsen, 1982
1 to 2	Zekri, 1984
3.3 to 20	Vu et al., 1986
1.3 to 25.2	Graser and Allen, 1987
0.5 to 10.2	Graser and Allen, 1988

difference (Hall et al., 1975; Khairi and Hall, 1976a,b; Kaufmann and Levy, 1976; Levy, 1980; Levy and Syvertsen, 1981; Zekri,1984; Vu et al., 1986).

Much effort has been made to relate stomatal activity of a number of plant species, including citrus, to plant water stress as measured by leaf xylem water potential (Kaufmann and Levy, 1976; Syvertsen et al., 1981, Syvertsen, 1982; Zekri, 1984; Zekri and Parsons, 1988). While measurements of this sort have been used in instances to conclude that stomatal conductance decreases in response to a critical leaf water potential, it is apparent that a unique relationship does not exist between the two variables. Furthermore, numerous studies with species other than citrus show a lack of close relationship between stomatal conductance and bulk leaf water potential (Blackman and Davies, 1985; Gollan et al., 1985; Osonubi, 1985; Bennett et al., 1987). Several reasons appear to be largely responsible for this lack of relationship. The first is related to the ability to accurately measure the primary controlling factor of stomatal activity: guard and epidermal cell turgor. The hydraulic relationship between the epidermis and mesophyll tissue is not clearly understood at this time. Several studies have used the micropressure probe to detect differences between mesophyll and epidermal cell turgor potentials (Shackel and Brinkman, 1985; Frensch and Schulze, 1987). Generalized use of bulk leaf water potential measurements or leaf xylem pressure potential measurements as indicators of guard cell water status is therefore questionable (Schulze, 1986). The second reason for the absence of a unique relationship between leaf water potential and stomatal activity is that little is known about interactions between external conditions, leaf water status, and stomatal conductance, or the way in which guard cells integrate previous growing conditions or stresses.

Few, if any, data have been reported upon which to evaluate the relationship between stomatal activity in citrus and soil water status. Stanhill (1970) related values of citrus canopy resistance calculated from Penman's equation for potential evapotranspiration, with measurements of soil water potential in the upper 80 cm of a sandy soil. Subsequent studies have interpreted measurements of soil water status and stomatal conductance in terms of a cause-effect relationship mediated by plant water potential. Recently however, data obtained with several different species in separate studies showed that stomata responded directly to soil water status while the relationship between leaf conductance and leaf water potential was less definite (Bates and Hall, 1981,1982; Turner et al., 1984, 1985; Osonubi, 1985; Gollan et al., 1986). The proposed mechanism for stomatal closure in response to soil drying is reduced metabolic activity of roots resulting in decreased production of cytokinins that have been shown to promote stomatal opening while counteracting the effect of abscisic acid in the leaves (Coutts, 1981; Blackman and Davies, 1985; Schulze, 1986). Direct response of citrus stomata to soil water depletion requires further investigation.

Many plant species exhibit stomatal sensitivity to the water vapor concentration difference between the leaf and the air (Sheriff, 1977; Turner et al., 1984). The question that arises when attempting to understand this behavior is whether stomata close in response to reductions in mesophyll tissue turgor brought about by increased rates of transpiration or whether stomata respond directly to atmospheric evaporative demand. Hypothesized mechanisms for these responses involve changes in epidermal turgor brought about by changing resistances in the pathway for flow of water between the mesophyll and the epidermis and regulation of epidermal turgor by cuticular transpiration. Details of these mechanisms have been discussed by Schulze (1986). Work by Turner et al. (1984) using several herbaceous and woody species illustrates some of the difficulty in separating leaf conductance response to internal and external conditions. Their work also indicated that in addition to a response to bulk leaf water potential, leaf conductance of the woody species studied responded directly to vapor pressure deficit of the air. Work with citrus has largely served to substantiate the claim of stomatal sensitivity to atmospheric evaporative demand but the particular mechanisms involved have yet to be elucidated. Work with citrus as well as other species also indicates that stomatal sensitivity is strongly influenced by previous growing conditions (Hall et al., 1975; Kaufmann and Levy, 1976).

It has long been noted that water use by citrus is unexpectedly low compared to that of other crop species, both herbaceous and woody (Van Bavel, 1967; Mantell, 1977; Meyer and Green, 1981). This lower water use characteristic, which enables many citrus species to grow well in both humid and arid environments, is frequently attributed to stomatal sensitivity to leaf-to-air humidity deficits resulting in constant or steadily declining transpiration rates during the course of a day despite increasing radiation and atmospheric vapor pressure deficit. An aircraft-borne thermal infrared scanner image showed that citrus canopy temperatures of a 250-ha grove of grapefruit and orange tree were about 3.3 °C warmer than either mixed tall broadleaf hardwood and cabbage palm canopy temperatures or mixed short broadleaf hardwood and broadleaf shrub canopy temperatures near midday in late April 1978 in Okeechobee County, Florida (L.H. Allen, Jr., personal communication). Furthermore, the citrus canopy temperatures were about 1.8 °C above weather shelter-height air temperature (24.3 °C) whereas the other tall canopies were about 1.5 °C below air temperature. These foliage-to-air temperature differences demonstrate a relatively larger stomatal resistance for citrus than for the other broadleaf tree and shrub vegetation, which should reduce water loss by transpiration.

Halevy (1956) showed that transpiration rates of Shamouti orange leaves on 'Sharav' days in Israel, which were characterized by high temperatures and relative humidity less than 10%, did not exceed rates obtained on 'normal' summer days. Hilgemann (1966) reported nearly equivalent water use by citrus leaves grown under differing evaporative demand conditions in Arizona and Florida. Also in Israel, Stanhill (1970) determined citrus canopy water use to be less than one-quarter of its climatically determined potential, as indicated by actual to potential evapotranspiration ratios. Hall et al., (1975) reported that maximum transpiration rates of sweet orange seedlings per unit leaf area remained nearly constant at about 2.5 $\mu g\ cm^{-2}\ s^{-1}$ (1 $\mu g\ cm^{-2}\ s^{-1}$ = 10 $mg\ m^{-2}\ s^{-1}$ = 0.555 $mmol\ m^{-2}\ s^{-1}$) under increasing vapor pressure deficits. Transpiration rates of leaves of plants acclimated to higher vapor pressure deficit increased to about 4.5 $\mu g\ cm^{-2}\ s^{-1}$. These values agree well with transpiration rates of lemon which ranged from 2.0 to 4.0 μg cm^{-2} leaf area s^{-1} over increasing absolute humidity deficits (Levy, 1980). Weighing lysimeter measurements of transpiration from whole Valencia citrus trees showed a nearly constant rate of 8.3 μg cm^{-2} ground area s^{-1} between 0930 and 1530, approximately equal to leaf rates of 1.9 μg cm^{-2} s^{-1} (Meyer and Green, 1981). Maximum transpiration rates of 12.1 to 7.4 μg cm^{-2} leaf area s^{-1} for well watered and water stressed field-grown, young Hamlin trees were reported by Marler (1988).

Photosynthesis

Concern over water availability and use by plants is ultimately related to the effects of water stress on photosynthesis and consequent effects on plant growth. Photosynthetic rates of well-watered citrus are characteristically low compared to other woody perennials (Kriedemann, 1968, 1971; Downton et al., 1987). Thompson et al. (1965) found leaf photosynthetic rates of rough lemon (C. jambhiri) seedlings of about 3.5 μmol CO_2 m^{-2} s^{-1} (units converted). Kriedemann reported values of about 6.3 μmol CO_2 m^{-2} s^{-1} (units converted) for attached leaves of both orange and lemon in 1968 and slightly higher rates, 6.3 to 7.6 μmol CO_2 m^{-2} s^{-1} (units converted) for orange leaves alone in 1971. Khairi and Hall (1976 a,b) reported maximum leaf photosynthetic rates over a range of leaf temperatures and leaf to air vapor pressure differences of 2.0 to 12.8, 2.5 to 10.9 and 5.9 to 12.1 μmol CO_2 m^{-2} s^{-1} for grapefruit (C. paradisii), orange and lemon, respectively. Field-grown citrus trees in Florida with leaf photosynthetic rates of 6 to 11 μmol CO_2 m^{-2} s^{-1} were reported by Sinclair and Allen (1982). Slightly higher maximum rates, 10 to 15 μmol CO_2 m^{-1} s^{-1}, were reported in a study of leaves of healthy and blighted Valencia trees in Florida (Sinclair et al., 1983). Marler (1988) measured maximum leaf CO_2 assimilation rates of 12.7 and 8.1 μmol CO_2 m^{-2} s^{-1}, respectively, on well-watered and water-stressed Hamlin trees in the field. In a study of CO_2 enrichment effects on citrus photosynthesis, leaves existing prior to initiation of treatments had rates of 4 to 6 μmol m^{-2} s^{-1} and leaves expanded after treatments began had rates of 8 to 9 μmol m^{-2} s^{-1} (Downton et al., 1987). Vu and Yelenosky (1988) reported maximum photosynthetic rates of 7.8 and 4.5 μmol CO_2 m^{-2} s^{-1} for control and water-stressed Valencia leaves, respectively.

Many studies indicate that water deficit induced reductions of photosynthetic rates are well correlated with stomatal closure (Boyer, 1976; Hsiao, 1973). A number of nonstomatal factors have also been shown to control CO_2 assimilation. These include CO_2 dissolution at the cell wall, transport in solution to the chloroplast, and the state and activity of pertinent enzymes. These factors, together referred to as mesophyll resistance, have been shown to be sensitive to environmental and physiological conditions, including water stress (Hsiao, 1973). Kriedemann (1971) attributed the low base photosynthetic rates of citrus in large part to high mesophyll resistance. Reduction of assimilation rates in citrus in response to water stress has been reported by Thompson et al. (1965), Bielorai and Mendel (1969) and Marler (1988). Vu and Yelenosky (1988) suggested the relative role of stomatal and nonstomatal factors influencing photosynthesis of water-stressed and nonstressed Valencia orange leaves. Inhibition of ribulose 1,5-bisphosphate carboxylase activity due to reduction in activation state and enzyme concentration in water stressed compared to nonstressed leaves were determined to be largely responsible for lowered photosynthetic rates in the stressed treatment. But, whereas rates declined in both treatments in the afternoon, enzyme activities in both treatments measured in the afternoon were determined to be adequate to support photosynthetic rates observed in the morning. Afternoon depression of CO_2 assimilation was attributed to reduced stomatal conductance.

Midday depression of leaf photosynthesis was reported in potted sour orange (C. aurantium) and sweet lime (C. limettioides) at high, as well as low, soil water contents and was followed by slight increases in photosynthetic rate in the afternoon (Bielorai and Mendel, 1969). Midday depression of photosynthesis in field grown citrus on a Spodosol in Florida was determined to occur on days with maximum temperatures of 31 °C or greater and atmospheric vapor pressure deficits greater than 3.0 kPa. (Sinclair and Allen, 1982). Soil water status was not described in this study, but the water table was low (about 1 m) and surface irrigation was withheld during the study (L.H. Allen, personal communication, April 1989). Midday depression of CO_2 assimilation in Prunus armeniaca was measured under conditions of elevated leaf to air vapor pressure difference and was attributed to stomatal closure (Schulze et al., 1974). Midday reduction of photosynthesis is a well documented phenomena in many species found in arid environments and has been described as an adaptive, water-conservative response of stomata to conditions of high temperatures and evaporative demand (Morrow and Mooney, 1974; Schulze et al., 1987; Tenhunen et al., 1981).

Models of Water Movement in the Soil-Plant-Atmosphere

Commonly used methods of measuring plant water deficits and scheduling irrigation are based on determinations of water status in the soil or plant or the relative rates of plant water use and atmospheric evaporative demand. Yet measurements in only one part of the soil-plant-atmosphere system may not be adequate to provide reliable estimates of water availability. Dynamic simulation of water flow in the SPAC has been used to investigate relationships between water status in the soil and plant in response to water use. Various approaches have been taken to describe the essential processes of water movement or uptake in the soil, evaporative demand, plant water status, and feedback mechanisms.

As mentioned earlier, models of water uptake by plant roots use either the microscopic perspective, in which soil water content or potential changes in the vicinity of the roots is considered, or the macroscopic approach. With the macroscopic approach the soil is typically divided into layers or compartments which reflect differences in root distribution or soil characteristics. Uniformity of soil properties and water content throughout each layer is assumed. Water movement in each layer is calculated by combining the Darcy-Richards equation for transient flow with a sink term describing water uptake by plant roots

$$\frac{\partial \theta}{\partial t} = \nabla \cdot [K(\psi) \nabla \cdot \psi_s] - S \qquad (2.16)$$

where S is the water extraction term for roots ($cm^3\ cm^{-3}$) and all other symbols are as previously defined. The water uptake term can be determined as a function of space, time, water potential, water content, amount and properties of roots, and transpiration rate or water use. Several workers have defined the extraction term using the microscopic model. Molz (1981) compiled water uptake terms from numerous models. Plant water use models utilizing the macroscopic approach to soil water extraction include those by Ogata et al. (1960), Nimah and Hanks (1973), Running et al. (1975), Van Bavel and Ahmed (1976), Federer (1979), Zur and Jones (1981), Stroosnijder (1982) and Hoogenboom et al. (1987). Plant water use models incorporating the microscopic approach include those by Cowan (1965), Feddes and Rijtema (1972) and Lambert and Penning de Vries (1973).

Whereas models having the limited objective of analysis of soil water movement and soil water profiles often use constant flux or demand terms, models of water movement in the soil-plant-atmosphere incorporate variable demand functions. Evaporative demand may be calculated from environmental conditions using Penman's equation for potential transpiration (Penman, 1948) as modified by Monteith (1965)

$$L_vE = \frac{\Delta\ R_n\ +\ C_p\ \rho\ V/r_a}{\Delta\ +\ \gamma(r_c\ +\ r_a)/r_a} \tag{2.17}$$

where

R_n = net radiation, W m^{-2},

Δ = slope of saturation vapor pressure curve at T, kPa $°K^{-1}$,

C_p = specific heat of air, J kg^{-1} $°K^{-1}$,

ρ = density of air, kg m^{-3},

V = atmospheric vapor pressure deficit, kPa,

r_a = boundary layer resistance, s m^{-1},

γ = psychometric constant, kPa °K^{-1}, = $(P\ C_p)/[\lambda(m_w/m_a)]$

where, P = atmospheric pressure, kPa,

λ = latent heat of vaporization, J kg^{-1},

m_w/m_a = ratio of molecular weight of water to molecular weight of air,

r_c = canopy resistance, s m^{-1},

L_v = latent heat of vaporization, J m^{-3},

E = transpiration rate, m s^{-1}.

Cowan (1965), Federer (1979) and Zur and Jones (1981) are some examples of models using the Penman-Monteith equation, or modifications thereof, to determine water use of a hypothetical crop, a hardwood forest, and soybean (Glycine max), respectively. Running et al. (1975) calculated transpiration using the leaf-to-air absolute humidity deficit, and leaf characteristics of Douglas fir (Pseudotsuga menziesii (Mirb) Franco):

$$T_d = D_a \cdot (1/r) \cdot L_d \cdot A_l \qquad (2.18)$$

where

T_d = transpiration, liters day^{-1},

D_a = absolute humidity deficit, liters m^{-3} air,

r = leaf resistance, s cm^{-1},

L_d = day length, seconds,

A_l = leaf area, cm^2.

Expression of leaf resistance in s m^{-1} rather than s cm^{-1} and leaf area in m^2 rather than cm^2 results in transpiration in liters day^{-1}.

The leaf resistance term commonly acts as the feedback mechanism between soil water and atmospheric humidity deficit conditions and plant water loss. Many models of water movement in the soil-plant-atmosphere continuum describe stomatal conductance as a single function of leaf water potential. This relationship frequently takes the form of a constant linear decline in stomatal conductance as water potential decreases or, a constant stomatal conductance as water potential decreases until a threshold is reached, followed by a steady, linear decline, or as a constant curvilinear decline (Jarvis, 1976; Turner et al., 1978). But, in light of the results of a number of recent studies, it is evident that there is no basis for assuming a direct, unique relationship between stomatal conductance and leaf water potential (Hall, 1982; Turner et al., 1984; Passioura, 1982).

Other models have attempted to relate stomatal conductance to soil and atmospheric conditions, as well as plant water status. Jarvis (1976) stated that a satisfactory approach to simulating stomatal response to environmental variables depends on knowledge of the mechanisms involved at the cellular level that is presently not available. Therefore, he proposed a phenomenological approach to modeling stomatal activity that utilizes known relationships between stomatal conductance and individual environmental factors such as temperature (T), intercellular CO_2 concentration (CO_2), radiation (I), humidity deficit (H), and leaf water potential (ψ_L). But, because the influence of interactions between these variables on stomatal conductance is not known, this approach assumes the complete expression of the influence of individual variables combined in a multiplicative manner without synergistic interactions, namely

$$g_s\ (T,I,H,\psi_L,CO_2) = g_s(T) \cdot g_s(I) \cdot g_s(H) \cdot g_s(\psi_l) \cdot g_s(CO_2) \qquad (2.19)$$

Shawcroft (1971) previously described an approach to predicting stomatal conductance as a function of radiation and plant water status which included an hypothesis of the form of their interaction. Stomatal resistance as a function of radiation was described assuming Michaelis-Menten kinetics with the equation

$$r_s = a + \frac{b}{(I + I_o)} \qquad (2.20)$$

where a is variable representing minimum stomatal resistance that depends on plant water status. Stomatal resistance response to radiation thus provided the basis of the description and interaction with plant water status was essentially a linear increase in the maximum resistance as water stress increased.

The approach used by Running et al. (1975) predicts stomatal conductance in response to plant water status and incorporates a threshold response to leaf-to-air humidity deficit. Federer (1979) described stomatal resistance as a function of radiation, temperature, humidity deficit, and plant water potential in an additive manner. Grantz and Zeiger (1986) derived equations for predicting the interactive effects of radiation and humidity deficit on stomatal conductance. An inverse relationship between stomatal response to the two variables of the form

$$g_s = a + \frac{b(I^c)}{(V^d + e)} \qquad (2.21)$$

where

I = photon flux density,

V = leaf-to-air vapor pressure deficit,

b,c,d,e = coefficients determined using nonlinear regression.

was found to more accurately predict stomatal conductance than descriptions using additive terms alone.

In light of the above discussion of what is known about stomatal response to individual environmental factors, and what is not known about the response of stomata to interacting factors, it is evident that stomata represent a critical but poorly understood component in the regulation of water movement in the soil-plant-atmosphere continuum.

CHAPTER III

GAS EXCHANGE RESPONSES OF CITRUS SEEDLINGS TO TEMPERATURE, VAPOR PRESSURE DEFICIT, AND SOIL WATER CONTENT

Introduction

It is believed that progenitors of cultivated species of the genus Citrus originated in humid tropical parts of China, N.E. India, the Philippines, and Indonesia (Webber, 1948; Zukovskij, 1962; Reuther, 1977; Cameron and Soost, 1976). The mesophytic nature of the genus is reflected in a number of growth characteristics that have been interpreted by various workers as adaptations to its native, moist, understory environment. The relatively shallow, spreading rooting habit of many Citrus species is suited to thin, well-drained soils well supplied with moisture throughout the year (Reuther, 1977). That the smooth, waxy cuticle of its flat, broad leaves is important primarily as a barrier to water penetration and nutrient leaching (Tukey, 1980) concurs with the lack of xeropytic features for inhibiting water loss from leaves or from the thin, succulent bark of its twigs (Webber, 1948). Possingham (1980) reported that although the high stomatal frequency of Citrus leaves equips them for potentially high rates of transpiration, venation is poorly developed. Transpiration rates may be limited as well by the low absorptive capacity of the suberized root system which lacks abundant root hair growth (Castle, 1980; Kriedemann and Barrs, 1981). Syvertsen and Graham (1985) reported a close correlation between the transpiration rate and root hydraulic conductivity of five citrus rootstocks. De Villiers (1939) reported large differences in the hydraulic conductivity of stems of rough lemon, grapefruit and sour orange which were related to vessel diameter within each species.

Webber (1948) pointed out that feral groves of citrus that established in Florida soon after its introduction were typically found on rich, low, moist lands usually near lakes or rivers. These areas were grown up to forests of live oak, magnolia, and other tree species. Here citrus grew in the understory and formed dense thickets. The primary characteristics of these environments were an abundance of moisture, rich soil, and shade. But despite its mesophytic nature, commercial cultivation of citrus is extremely successful in subtropical areas where rainfall is seasonal, as well as in semi-arid and arid regions. While irrigation is a must under such conditions, the conservative water use characteristics of citrus undoubtedly constitute an important factor in its successful adaptation to these areas.

Most widely recongnized and studied among these characteristics has been stomatal closure of citrus in response to increasing leaf-to-air humidity deficits that results in low, often nearly constant, transpiration rates (Levy, 1980; Levy and Syvertsen, 1981; Hall et al., 1975; Kaufmann and Levy, 1976; Van Bavel, 1967; Halevy, 1956; Sinclair and Allen, 1982; Vu and Yelenosky, 1988). While this water conservative growth characteristic has undoubtedly permitted its habitat to be extented to regions more arid than its place of origin, the response of citrus photosynthesis to conditions of high temperatures, high evaporative demand, and low soil water availability has been less well characterized.

Photosynthetic rates of nonstressed citrus have been described as low compared to other woody perennials (Kriedemann, 1968, 1971; Downton et al., 1987). Another frequently reported characteristic of citrus photosynthesis is the occurrence of midday depression (Bielorai and Mendel, 1969; Sinclair and Allen, 1982; Marler, 1988; Vu and Yelenosky, 1988) Midday depression of photosynthesis is a well documented phenomena is many species found in arid environments and has been described as an adaptive, water conservative response of stomata to conditions of high temperatures and evaporative demand (Schulze et al., 1974; Morrow and Mooney, 1974; Tenhunen et al, 1981; Schulze et al., 1987).

Whereas transpiration is controlled primarily by stomatal activity when the boundary layer resistance to water vapor transport at the surface of the leaf remains constant, photosynthesis in affected by a number of factors in addition to stomatal aperature which are referred to collectively as nonstomatal factors or mesophyll resistance. Among these nonstomatal factors are: CO_2 dissolution in the cytoplasm and transport to the chloroplast, the state and activity of pertinent enzymes, and photochemical activity (Hsiao, 1973). Although the contribution of nonstomatal factors to midday depression of citrus photosynthesis has been recognized (Bielorai and Mendel, 1969; Sinclair and Allen, 1982; Vu and Yelenosky, 1988; Marler, 1988) the relative importance of stomatal and nonstomatal factors is unclear. Relatively little work has been conducted to determine the relative importance of stomatal and nonstomatal factors contributing to low photosynthetic rates and midday depression of photosynthesis in citrus or how they are influenced by the environment.

Measurement of the relative responses of citrus photosynthesis and transpiration responses of citrus to temperature, atmospheric vapor pressure deficit, and soil water status is the first step in understanding how basic physiological processes are affected by these environmental factors. This information is necessary in developing irrigation practices that are both water conservative and noninhibitory to plant growth. Thus, the objectives of this preliminary study were: a) to formulate a basic understanding of the relative responses of photosynthesis, transpiration, and water-use efficiency of fully irrigated citrus seedlings over a range of atmospheric and soil moisture conditions at both ambient and elevated CO_2 concentrations and b) to identify environmental conditions conducive to midday depression of photosynthesis.

Materials and Methods

Two-year old unbudded Carrizo citrange (*Poncirus trifoliata* x *Citrus sinensis*) and Swingle citrumelo (*P. trifoliata* x *C. paradisii*) seedlings were grown in greenhouses in 2-L metal containers using a loam potting medium. On 9 April 1985, 72 containers of each rootstock cultivar were placed separately in each of two computer-managed, sunlit, controlled environment chambers. The resultant canopy in each chamber was dense enough to intercept nearly all of the incoming radiation. A Li-Cor light bar was placed in each chamber to measure photosynthetically active radiation penetration through the canopy during the study. The chambers, described in detail by Jones et al.

(1984), have been used to study season-long plant responses to elevated carbon dioxide (CO_2) concentrations. The east, west, and south walls of the growth chambers were constructed of Mylar polyester film and the top of a rigid plate of cellulose acetate. This whole portion of the transparent chamber was easily removed for access to the plants. The rigid north wall was constructed of acrylic material and contained exit and entry plenum for ductwork that housed air conditioning equipment (blowers, chilled-water cooling coils, and electrical resistance heaters). The transparent top and walls allowed 88% of the natural solar radiation to enter. Dry-bulb and dewpoint temperatures and CO_2 concentration were measured and controlled in the canopy zone. A schematic of the environmentally controlled chambers and associated ductwork is shown in Appendix A.

The containers, with ports near the bottom for drainage and flood irrigation, were placed in shallow (1 m x 2m x 0.15m) trays in the chambers. Irrigation was provided by flooding the trays for about two hours near sunset and draining the trays (and containers) overnight. Most of the excess water had drained or evaporated by morning. Bathroom scales fitted with linear variable displacement transducers with remote digital readout units were used to measure daily weight changes due to transpiration. Total soil water of containers in each chamber was determined by recording the weight of the plants plus containers the morning following an irrigation and subtracting the weight they attained when temporary leaf wilting was observed. The percentage available soil water (ASW) remaining each morning and evening was determined by subtracting from the total soil water the amount of water collected each morning and evening as cooling coil condensate that dripped in to a closed container. Reported values were represent values measured in the morning.

Treatments were applied to plants in both chambers simultaneously and consisted of a series of soil water depletion cycles overlaid by three levels of dry-bulb/dewpoint temperatures (DBT/DPT) and two levels of atmospheric CO_2 concentration. Water in the containers was allowed to be depleted until plants began to show signs of stress so that the number of days in a drying cycle varied according to the DBT level and CO_2 concentration. Dry-bulb temperature controls in the chambers were implemented as diurnal curves that paralled changes in solar radiation. Dewpoint temperatures were constant throughout 14-hour the daytime period beginning at 0600 and ending at 2000 EST. Maximum DBT and constant DPT control set points were 24/10, 29/14, 37/22 °C, for the low, intermediate, and high temperature levels, respectively. These temperature treatments included two levels considered to be within the optimum temperature range for citrus (low and intermediate) and one higher than the optimum temperature range (high). Temperatures maintained in the chambers were typically within 1 to 2 °C of the control set points. Night time DBT/DPT controls were set at 14/6, 16/14 and 22/14 °C, for low, intermediate, and high temperature treatments, respectively, for 10 hours beginning at 2000 and ending at 0600 EST. The diurnal maximum atmospheric vapor pressure deficits (VPD) resulting from low, intermediate, and high temperature treatments were 1.7, 2.4, and 3.6 kPa, respectively, and represent nonstress levels (low and intermediate) and stress levels (high). Treatments will be referred to simply as low, intermediate or high levels of DBT/VPD and indicate the maximum DBT/VPDs of 24/1.7, 29/2.4, and 37/3.6, respectively. The diurnal pattern of DBT/DPT control set points and the resultant atmospheric vapor pressure deficits are shown in Figure 3.1. The two CO_2 concentrations used were ambient, 330 μmol mol^{-1}, and 'elevated', 840 μmol mol^{-1}. During the last week of the approximately ten-week long study, citrus response to saturated or nearly saturated soils was evaluated by flooding to the rim the trays in which the containers were standing. Because the containers were approximately 10 centimeters taller than the top of the trays, complete submersion of the containers was not achieved. The trays were refilled as the water level fell. A schedule the dates of changes in the environmental conditions maintained in the chambers throughout the study is shown in Appendix B.

Real time canopy carbon dioxide exchange rates (CER) were measured by metering CO_2 to maintain a constant concentration (Jones et al., 1984) and are expressed per unit ground surface area of the chambers based on 2.0 m^2 for each chamber. Real time evapotranspiration rates (ET) were calculated from cooling-coil condensate removal rates, as measured by tipping-bucket rain gauges. Environmental variables: dry-bulb (DBT) and dewpoint temperatures (DPT), carbon dioxide (CO_2) concentration, and photosynthetically active radiation (PAR), measured at the top of the canopy inside the chambers, as well as gas exchange rates, were recorded throughout the day at 5-minute intervals. Data points shown here represent the average of twelve 5-minute interval readings during the indicated hour, i.e., the value reported for 9 EST represents the mean of 12 readings between 9.00 to 9.92 EST. Because gas

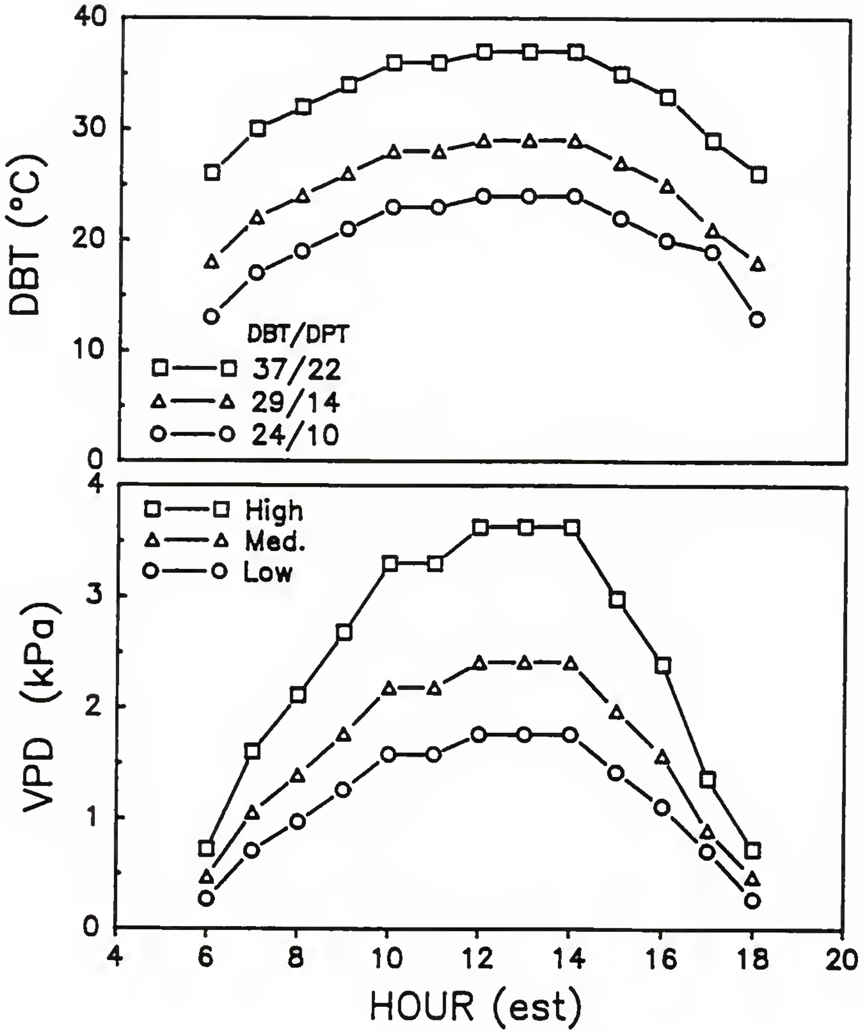


Figure 3.1. a) Diurnal dry-bulb/dewpoint temperature (DBT/DPT) control set points at the high, intermediate and low treatment levels. Maximum DBT and constant DPT for the three levels of control are listed in the legend.

b) Calculated saturation vapor pressure deficits (VPD) of the air at the high, intermediate, and low temperature levels.

exchange rates of the two rootstock cultivars were nearly identical, only data obtained from the chamber containing Swingle citrumelo are shown unless otherwise stated.

Results

Atmospheric and Soil Water Effects on Diurnal Gas Exchange

At each combination of the three levels of DBT/VPD and two levels of CO_2 concentration, the relative changes in CER and ET were evaluated at a 'high' and a 'low' level of ASW obtained during a soil drying cycle. The dates available for representation of these conditions were often limited by variable solar radiation or technical problems. Because solar radiation is a major environmental factor influencing both CER and ET, days with high radiation were selected for comparisions whenever this was possible. For this reason also, the diurnal PAR curve is included in plots of CERs. When it was not possible to compare gas exchange responses at high and low ASW levels on days with similar solar radiation levels, it is expected that the effects of soil water status will be confounded with the level of radiation and consideration of this possibility is included in the discussion.

The low DBT/VPD, ambient CO_2 treatment

At ambient CO_2 concentration the highest CERs occurred at the low DBT/VPD treatment. When the soil water content under these atmospheric conditions was high (67% ASW), CERs of 16 to 17 $\mu mol\ m^{-2}\ s^{-1}$ were maintained between 0800 and 1500 EST (Figure 3.2). When soil water was depleted to 7% ASW at this DBT/VPD level, CERs reached a maximum of 18.5 $\mu mol\ m^{-2}\ s^{-1}$ before 1200 EST and dropped throughout the remainder of the

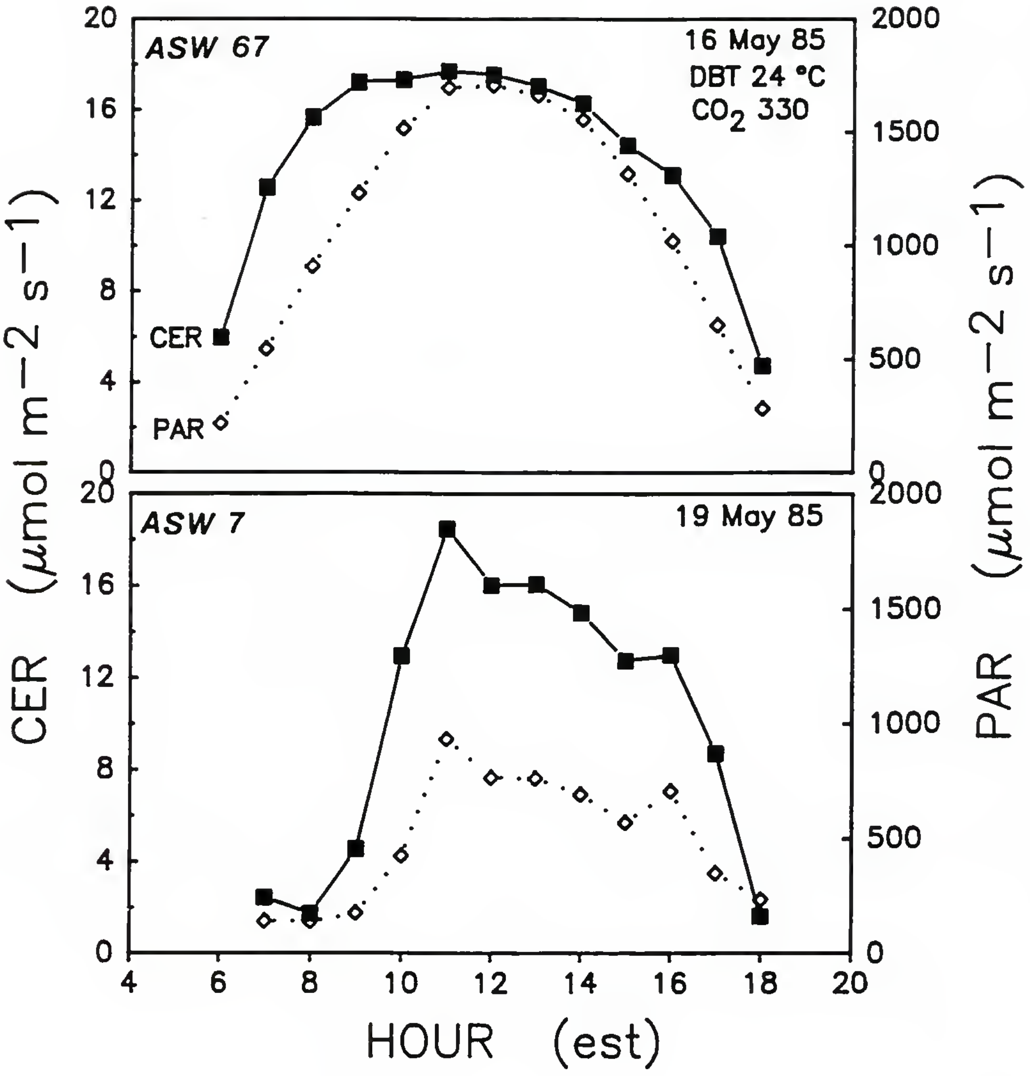


Figure 3.2. Carbon dioxide exchange rates (CER) of Swingle citrumelo citrus seedlings and diurnal photosynthetically active radiation (PAR) curves at the low dry-bulb temperature (DBT) level and ambient CO_2 (330 μmol mol^{-1}) concentration on days with high (67%) and low (7%) available soil water (ASW) contents.

day. Radiation levels also declined during the afternoon of this day and confound the effects of soil water level on gas exchange. It is apparent, however, that on this day high CERs occurred despite the low radiation (less than 1000 μmol m^{-2} s^{-1}) and low soil water content. Midday depression of photosynthesis was not observed at this level of DBT/VPD throughout the entire soil water depletion cycle in either rootstock.

Evapotranspiration rates at high soil water content in the low DBT/VPD treatment rose with increasing radiation and reached a maximum of approximately 7300 μmol m^{-2} s^{-1} (Figure 3.3). At the low ASW level ET also followed a diurnal pattern similar to that of radiation but maximum ET was only 4400 μmol m^{-2} s^{-1}. Low radiation throughout this day contributed to the lower ET rates compared to rates attained at the high ASW level.

High values of water-use efficiency (WUE) that occurred during the morning hours on 16 May resulted from the high values of CER and low ET at low radiation (Figure 3.4). Overall water-use efficiency under the low DBT/VPD conditions was higher on 19 May than on 16 May due to the relatively smaller reduction in CERs than in ET from 16 May, when radiation was high, to 19 May, when radiation was low. Again the low radiation on 19 May confounds the effect of low soil water (7% ASW) but these results emphasize the fact that at the low DBT/VPD level citrus CERs were high regardless of the level of ASW.

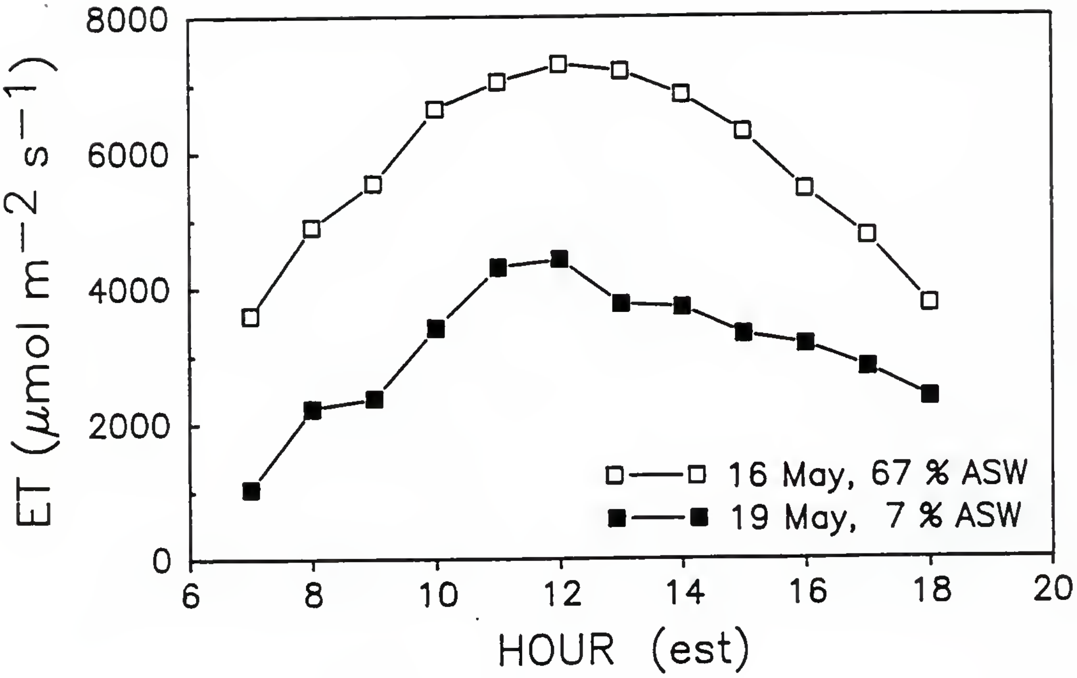


Figure 3.3 Evapotranspiration (ET) of Swingle citrumelo citrus seedlings at the low dry-bulb temperature level and ambient CO_2 concentration on day with high (67%) and low (7%) levels of available soil water (ASW).

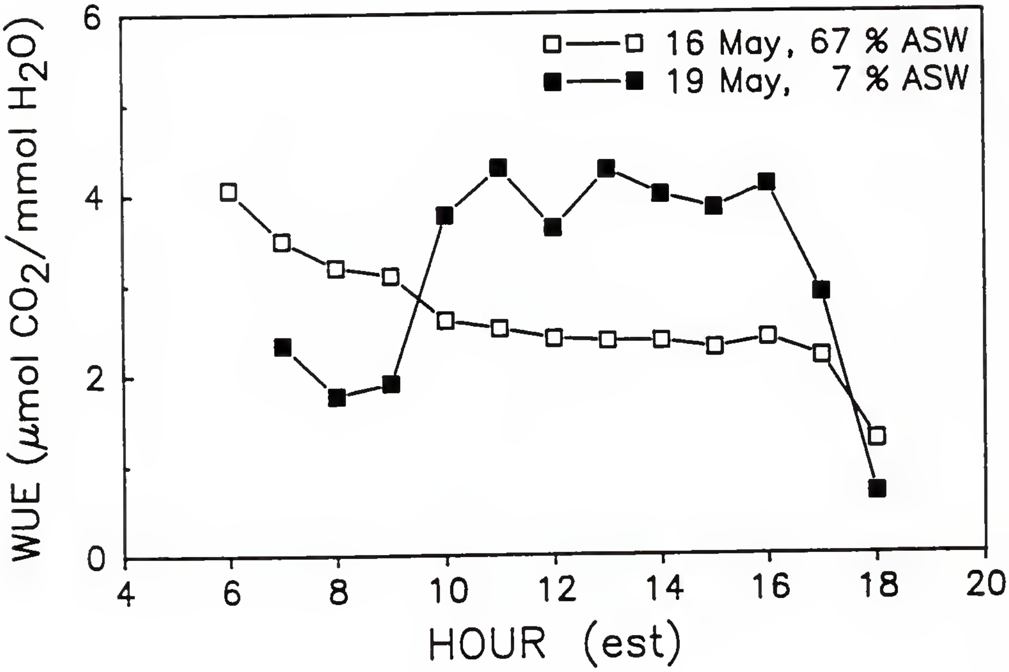


Figure 3.4. Water-use efficiency (WUE) of Swingle citrumelo citrus seedlings at the low dry-bulb temperature level and ambient CO_2 concentration on days with high (67%) and low (7%) levels of available soil water (ASW).

The intermediate DBT/VPD, ambient CO_2 treatment

At the intermediate DBT/VPD treatment,the maximum CER was in the range of 13.0 to 14.5 μmol m^{-2} s^{-1} and occurred before 1100 EST (Figure 3.5). Carbon exchange rates declined steadily during the remainder of the day although radiation remained high. This trend is depicted in Figure 3.5 for 23 April, when ASW was 56%. Similar diurnal trends that showed maximum CER occurring before 1100 EST and steadily declining or declining with a slight shoulder in the late afternoon were observed on other dates at this temperature level when ASW was greater than 90% (data not shown), and indicate that CERs of the citrus seedlings experienced some degree of stress in the afternoon at this DBT/VPD level. At the low soil water level (31% ASW), maximum CER was reduced to 12 to 13 μmol m^{-2} s^{-1} and began to decline soon after 1000 EST. Midday depression of photosynthesis was apparent at the intermediate DBT/VPD treatment when soil water contents were lower than 50% (data not shown).

Evapotranspiration at the intermediate DBT/VPD treatment and 37% ASW was not greatly reduced compared to that which occurred at 56% ASW (Figure 3.6). It appears that CERs were reduced to a greater extent by the 19% reduction in ASW than was ET.

Daily maximum and diurnal patterns of WUE were similar at the intermediate DBT/VPD level on the 23 and 24 April when ASW was 56 and 31%, respectively (Figure 3.7). The maximum WUE, about 4.5 μmol (CO_2) $mmol^{-1}$ (H_2O), occurred before 1000 EST on both days and declined during the middle of the day.

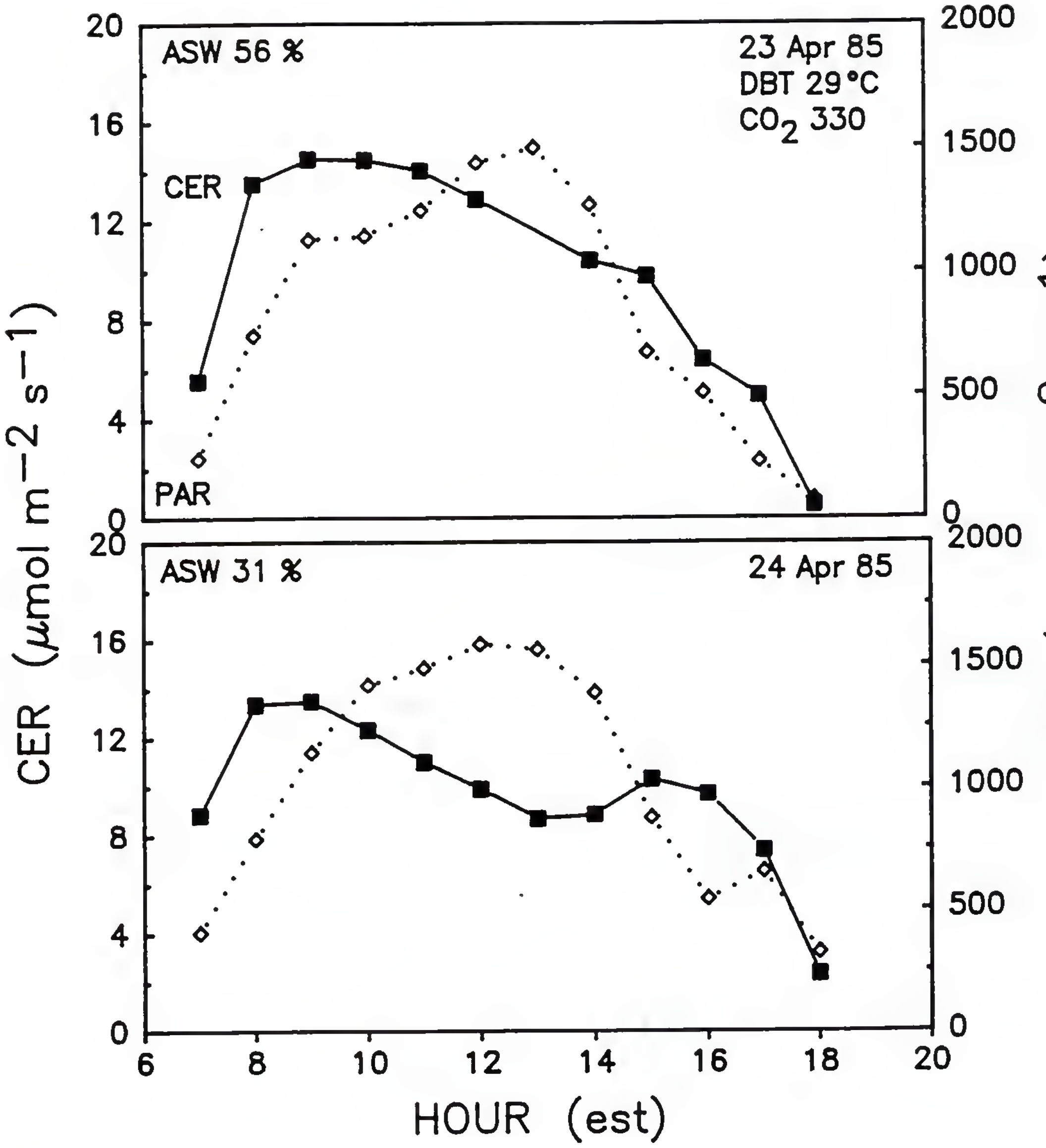


Figure 3.5. Carbon dioxide exchange rates (CER) of Swingle citrumelo citrus seedlings and diurnal photosynthetically active radiation (PAR) curves at the intermediate dry-bulb temperature (DBT) level and ambient CO_2 (330 µmol mol^{-1}) concentration on days with high (56%) and low (31%) levels of available soil water (ASW).

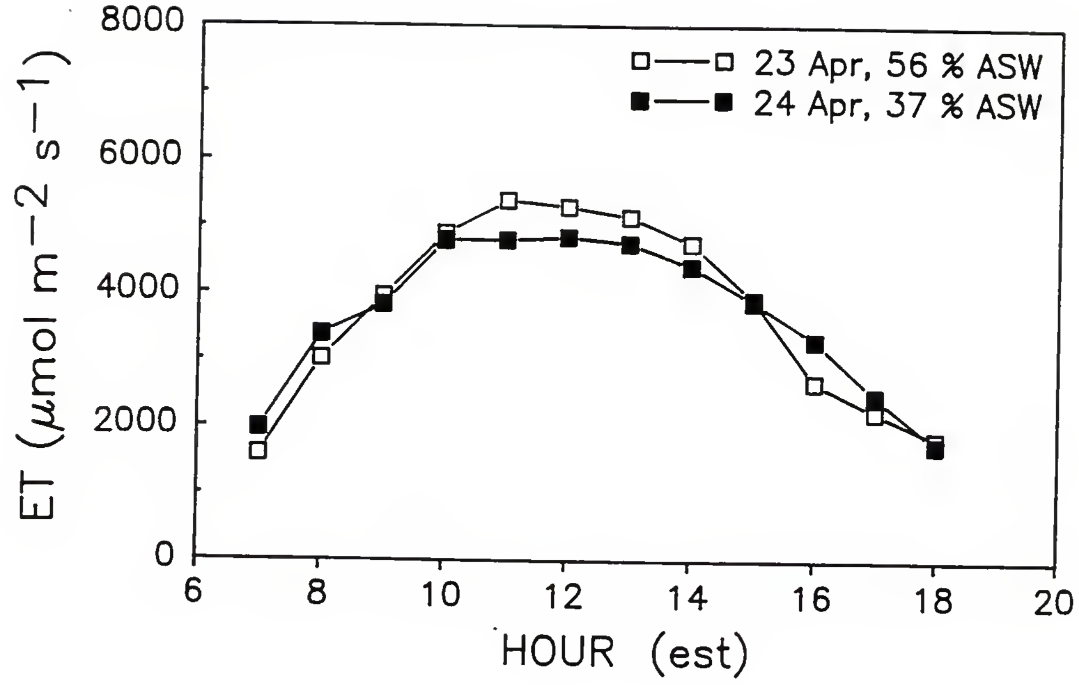


Figure 3.6. Evapotranspiration rates (ET) of Swingle citrumelo citrus seedlings at the intermediate temperature level and ambient CO_2 concentration on days with high (56%) and low (37%) levels of available soil water.

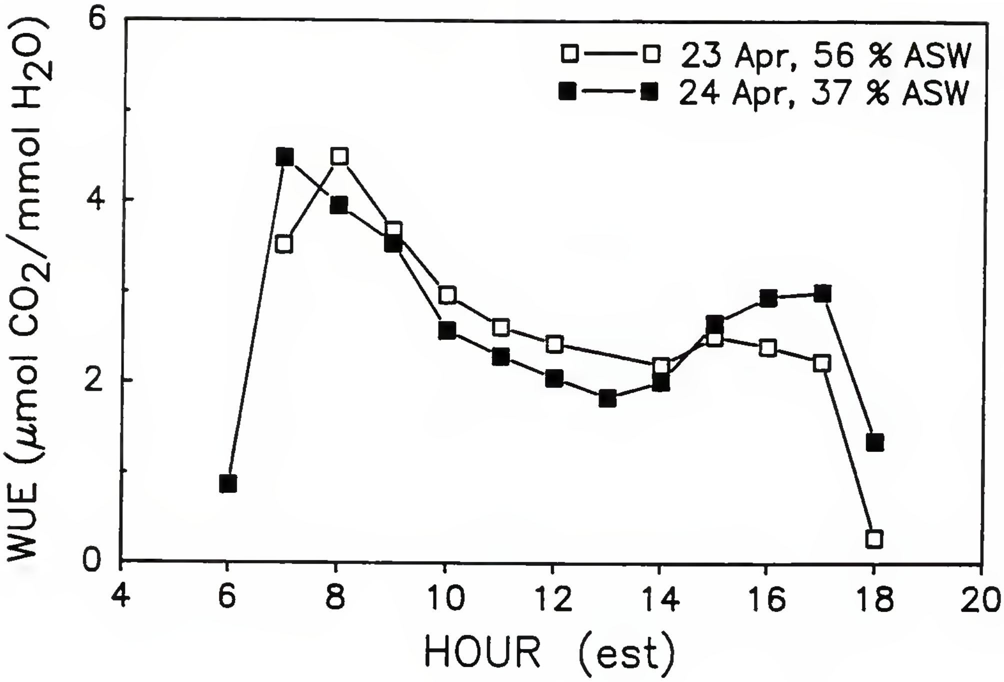


Figure 3.7. Water-use efficiency (WUE) of Swingle citrumelo citrus seedlings at the intermediate dry-bulb temperature level and ambient CO_2 concentration on days with high (56%) and low (37%) levels of available soil water (ASW).

The high DBT/VPD, ambient CO_2 treatment

Maximum CER under the high DBT/VPD treatment and high soil water content (64% ASW) was 10.5 μmol m^{-2} s^{-1} and was attained by 0900 EST (Figure 3.8). As radiation levels increased and remained greater than 1000 μmol m^{-2} s^{-1} between 0900 and 1500 EST, CERs remained in the range 9.5 to 10.5 μmol m^{-2} s^{-1} until decreasing rapidly between 1700 and 1800 EST. At the low soil water level (21% ASW) maximum CER was reduced to 7.4 μmol m^{-2} s^{-1} and this maximum occurred within the first two hours after sunrise. Typically, midday reduction and late afternoon recovery of CERs were observed under high DBT/VPD conditions when ASW fell below 60% (data not shown).

As expected, the highest rates of ET from the citrus canopy during the study were attained at the high DBT/VPD treatment and high ASW. Evapotranspiration rates rose throughout the day with increasing radiation to a maximum of nearly 9000 μmol m^{-2} s^{-1} (Figure 3.9). At the low soil water content ET rose to 5000 μmol m^{-2} s^{-1} at 0900 EST and remained nearly constant until 1400 EST.

Water-use efficiency was greatly reduced throughout the day under the high DBT/VPD conditions at both high and low levels of ASW (Figure 3.10) compared to values reached at low and intermediate levels of DBT/VPD (Figure 3.4 and 3.7). Morning WUEs on both the 11 and 13 May were less than 2.0 μmol CO_2/mmol H_2O (Figure 3.10).

The immediate effects of high DBT on CERs were apparent when DBT/DPT controls were switched from 29/14 °C to 37/22 °C between 1200 and 1400 EST on 25 April. Within ten minutes of the temperature change, net CERs of the Swingle plants dropped from 6.1 to 0.7 μmol m^{-2} s^{-1} and

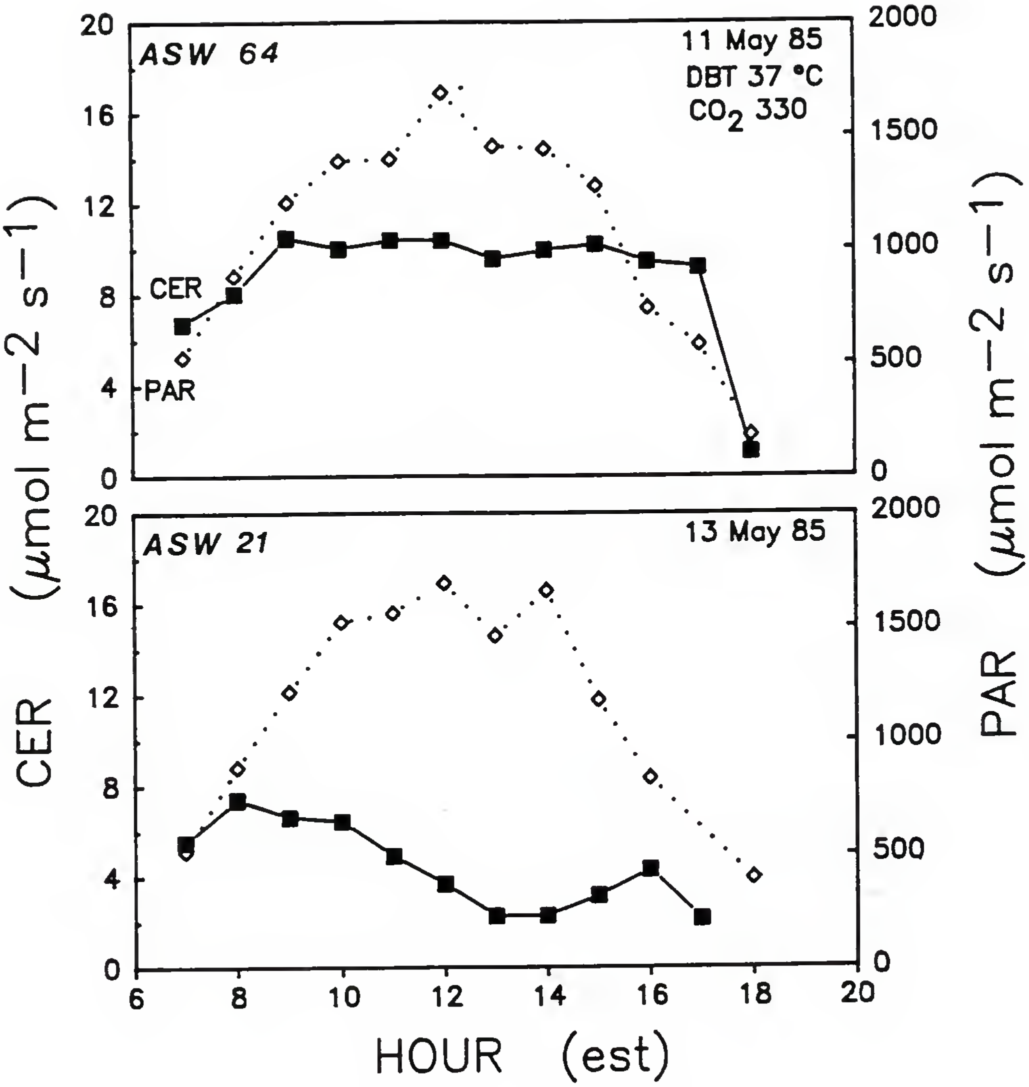


Figure 3.8. Carbon dioxide exchange rates (CER) of Swingle citrumelo citrus seedlings and diurnal photosynthetically active radiation (PAR) curves at the high dry-bulb temperature (DBT) level and ambient CO_2 (330 μmol mol^{-1}) concentration on days with high (64%) and low (21%) levels of available soil water (ASW).

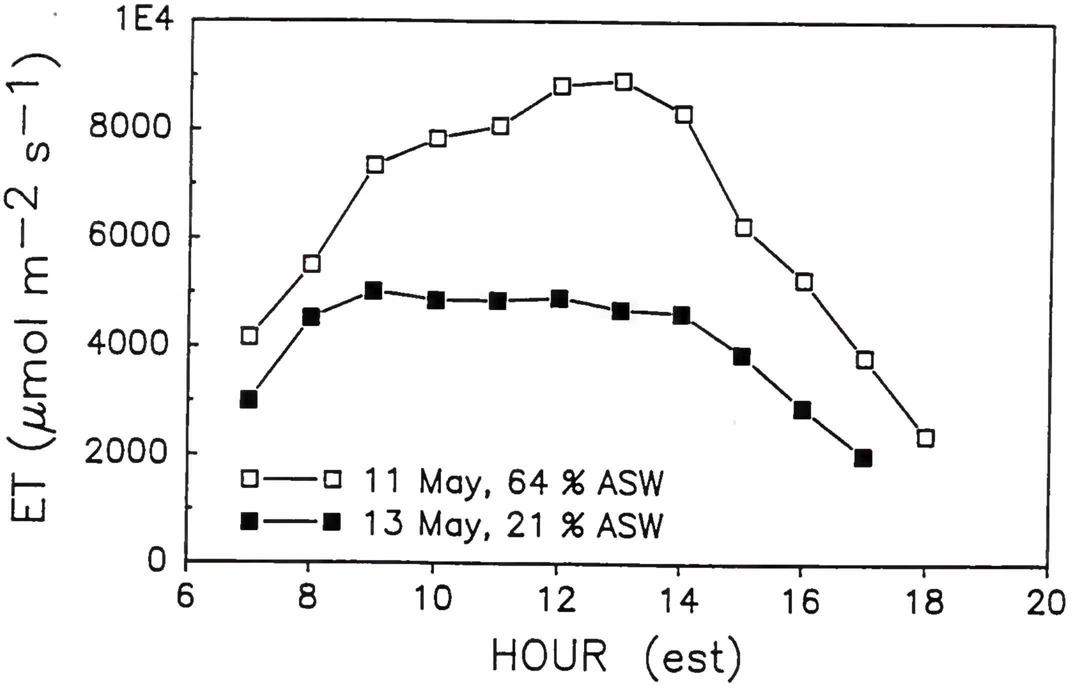


Figure 3.9. Evapotranspiration rates (ET) of Swingle citrumelo citrus seedlings and diurnal photosynthetically active radiation (PAR) curves at the high dry-bulb temperature level and ambient CO_2 concentration on days with high (64%) and low (21%) levels of available soil water (ASW).

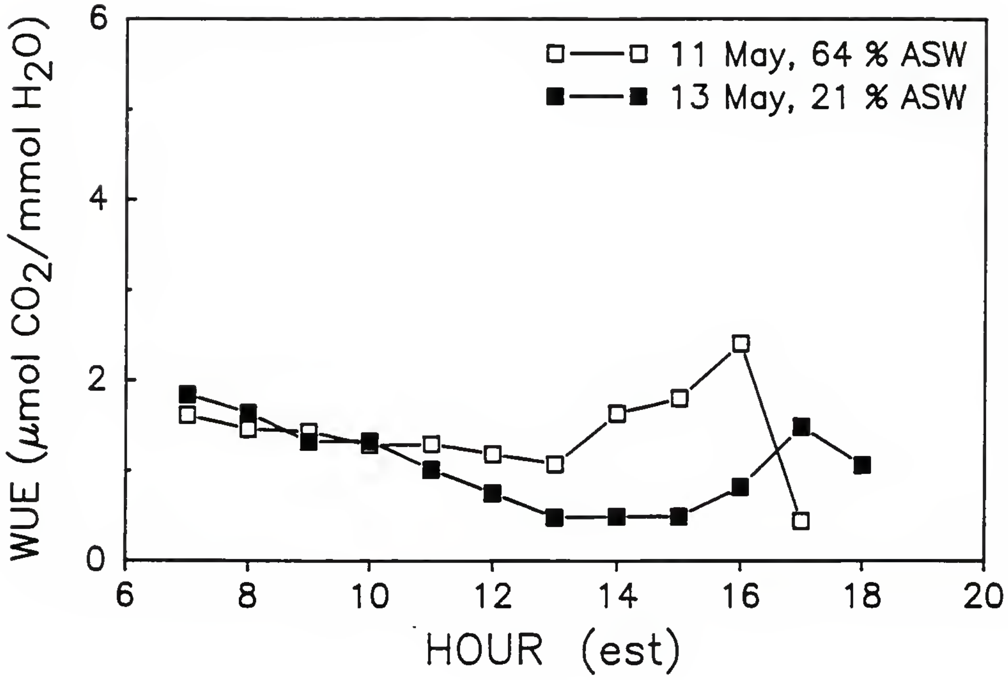


Figure 3.10. Water-use efficiency (WUE) of Swingle citrumelo citrus seedlings at the high dry-bulb temperature level and ambient CO_2 concentration on days with high (64%) and low (21%) levels of available soil water (ASW).

remained nearly constant at rates less than 1.0 μmol m^{-2} s^{-1} until temperatures were switched at 1400 EST to their previous levels (Figure 3.11). Carbon dioxide exchange rates of Carrizo citrange fell from 7.6 to 0.8 μmol m^{-2} s^{-1} within 25 minutes of the DBT/DPT change and were slightly higher than rates for Swingle citrumelo during the period of elevated temperatures (data not shown). Transpiration decreased from 4408 μmol m^{-2} s^{-1} just prior to the temperature change to a minimum of 3662 μmol m^{-2} s^{-1} during the two hours at 37 °C. Carbon dioxide exchange rates attained values approximately equal to those existing prior to the change within 25 minutes of reestablishment of previous temperatures.

On 7 June, the trays holding the pots were were filled with water, but because the containers were about 10 cm taller than the top of the water, it is unlikely that the soil was completely saturated. On the first day following flooding, CERs attained a maximum of 23.7 μmol m^{-2} s^{-1} before 1100 EST and declined slightly throughout the remainder of the day as radiation decreased (Figure 3.12). On 13 June, six days after the trays were filled, CERs remained high. Between 0900 and 1400 EST, CERs were in the range 20.0 to 23.1 μmol m^{-2} s^{-1}, indicating that plants were not under stress. Thus, midday depression of photosynthesis was not observed after six days under 'flooded', or nearly saturated soil conditions despite the high DBT/VPD level. On the evening of 13 June the trays were drained; no adverse effects of flooding were observed on CERs at any time during this period of flooding. The increase in CERs during the period of flooded conditions as compared to photosynthesis during the early part of the study was due at least in part to an increase in leaf area in the chambers.

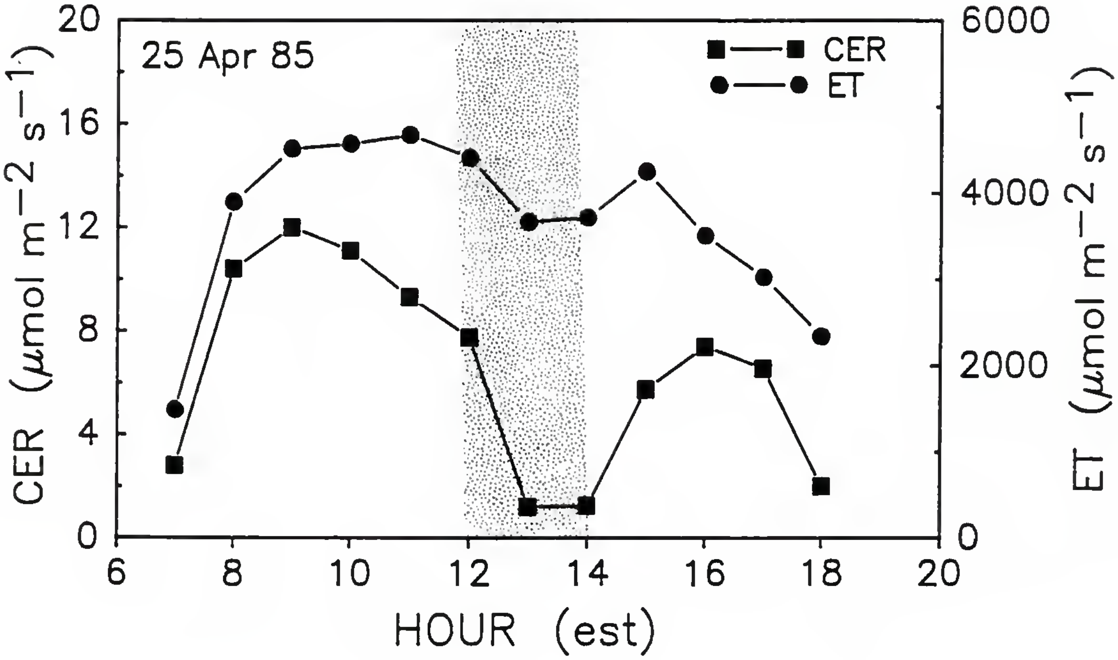


Figure 3.11. Carbon dioxide exchange rates (CER) and evapotranspiration rates (ET) of Swingle citrumelo citrus seedlings at the intermediate dry-bulb temperature level with short term exposure to the high dry-bulb temperature level. The darkened area indicates the period of high dry-bulb temperature.

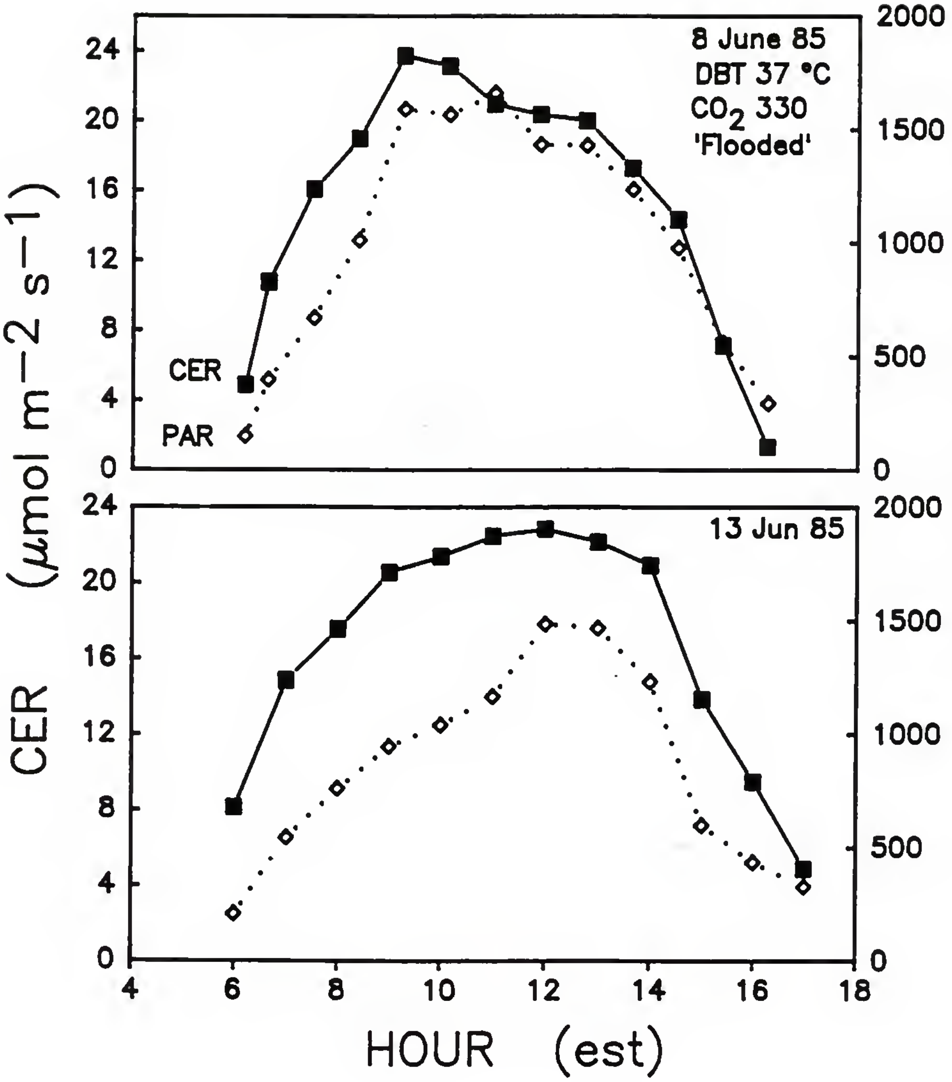


Figure 3.12 Carbon dioxide exchange rates (CER) of Swingle citrumelo citrus seedlings and diurnal photosynthetically active radiation (PAR) curves at the high dry-bulb temperature (DBT) level and ambient CO_2 (330 μmol mol^{-1}) concentration when the trays were flooded and the soil was nearly saturated.

The intermediate and high DBT/VPD, elevated CO_2 treatment

On 29 April, the CO_2 concentration in both chambers was increased to 840 μmol mol^{-1}. Maximum CERs at the intermediate DBT/VPD treatment and high soil water content (69% ASW) was 34.8 μmol m^{-2} s^{-1} (Figure 3.13). Between 0800 and 1500 EST, CERs remained within the range 30.0 to 34.5 μmol m^{-2} s^{-1}. At the low soil water level (18% ASW), maximum diurnal CER was reduced to 26.1 μmol m^{-2} s^{-1} and remained in the range of 21.2 to 26.1 μmol m^{-2} s^{-1} between 0800 and 1500 EST.

At the high DBT/VPD level and elevated CO_2 concentration, maximum CER at the high soil water level (70% ASW) was reduced to 25.6 μmol m^{-2} s^{-1}, as compared to more than 34 μmol m^{-2} s^{-1} at the intermediate DBT/VPD level, and remained nearly constant between 0900 and 1600 EST (Figure 3.14). At the low soil water level (13% ASW), the maximum diurnal CER was about 21.2 μmol m^{-2} s^{-1} and was attained before 1000 EST. Carbon dioxide exchange rates dropped slowly as radiation levels decreased during the remainder of the day. Midday depression of photosynthesis was not observed in plants subjected to the elevated CO_2 concentration regardless of air temperature or soil water level. At both levels of DBT/VPD, maximum CERs at the elevated CO_2 concentration and at high soil water contents was two fold greater than the maximum rates that occurred at their respective DBT/VPD level at the ambient CO_2 concentration.

At the elevated CO_2 concentration and intermediate DBT/VPD treatment, ET rose with increasing radiation throughout the day and reached a maximum of about 5500 μmol m^{-2} s^{-1} at the high soil water

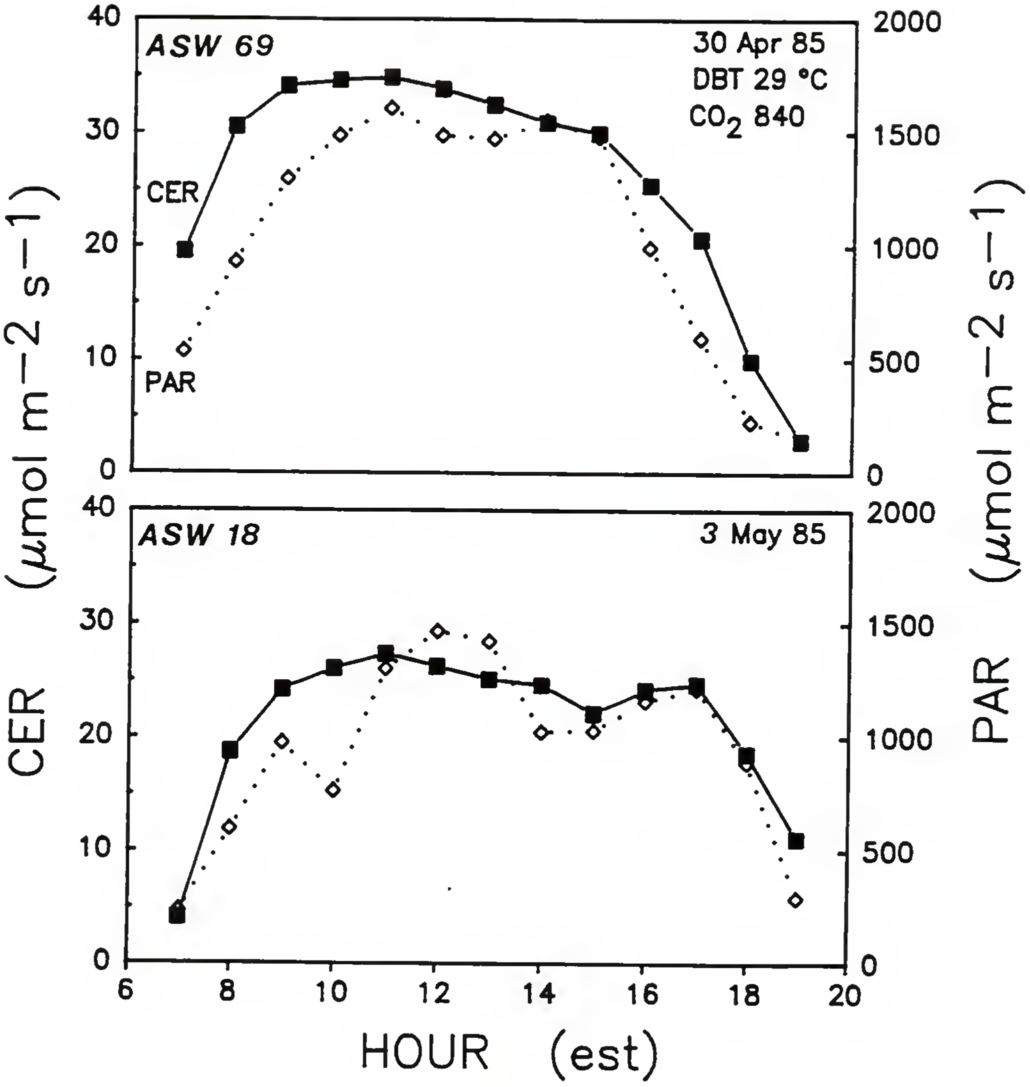


Figure 3.13. Carbon dioxide exchange rates (CER) of Swingle citrumelo citrus seedlings and diurnal photosynthetically active radiation (PAR) curve at the intermediate dry-bulb temperature (DBT) level and elevated CO_2 (840 µmol mol^{-1}) concentration on days with high (69%) and low (18%) levels of available soil water (ASW).

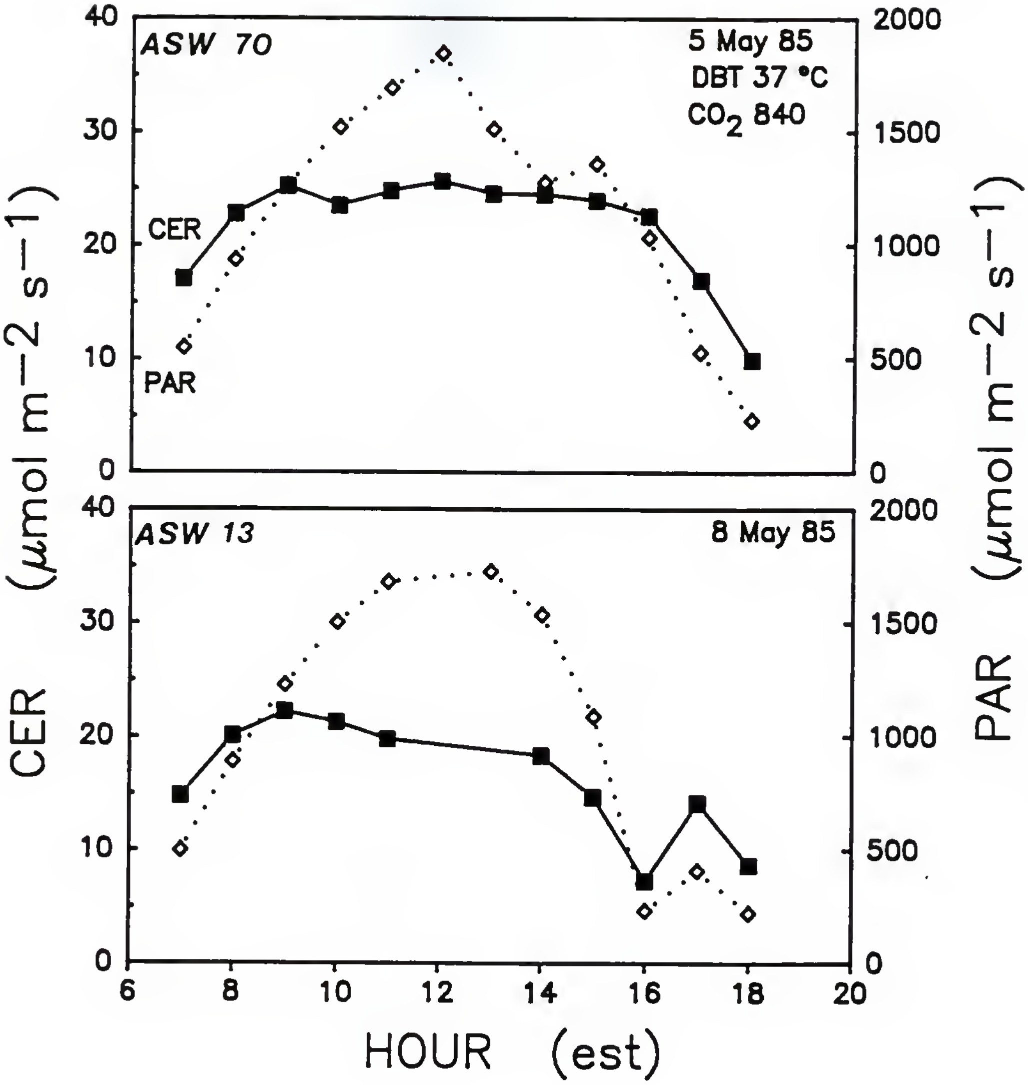


Figure 3.14. Carbon dioxide exchange rates (CER) of Swingle citrumelo citrus seedlings and diurnal photosynthetically active radiation (PAR) curves at the high dry-bulb temperature level and elevated CO_2 (840 μmol mol^{-1}) concentration on days with high (70%) and low (13%) levels of available soil water (ASW).

content and 4800 μmol m^{-2} s^{-1} at the low soil water content (Figure 3.15). At the high DBT/VPD level and high soil water content ET attained a maximum of 7600 μmol m^{-2} by 0900 EST and declined during the rest of the day. When the soil water level was reduced to 13% ASW, ET reached a maximum of about 4400 μmol m^{-2} s^{-1} by 0900 EST and remained quite constant until 1300 EST (Figure 3.16).

Water use efficiency at the high CO_2 concentration and intermediate DBT/VPD level was double that obtained at the ambient CO_2 level and was similar at both high and low levels of soil water (Figure 3.17). Under these conditons the reduction in WUE throughout the day was slight. With elevated CO_2 concentration and high DBT/VPD treatment, maximum midday WUE was reduced (Figure 3.18) to 4 to 5 μmol (CO_2) mmol^{-1} (mmol H_2O) compared to values of 7 μmol (CO_2) mmol^{-1} (H_2O) observed at the intermediate DBT/VPD.

Carbon Dioxide Exchange Rates Throughout the Soil Water Depletion Cycle

The effect of soil water depletion at each of the temperature and CO_2 concentration combinations is summarized in plots of the maximum and minimum CERs between the hours of 1000 and 1500 EST at the daily average ASW level throughout a particular soil drying cycle. Minimum CERs are included to indicate any increases in midday depression of photosynthesis that would not be reflected in the maximum CER values. Low values of radiation on the first day of several soil drying cycles prevented inclusion of those data. Roots of the two-year old plants filled the entire volume of the containers so that it can be assumed that essentially all of the soil water was extractable. This is evident

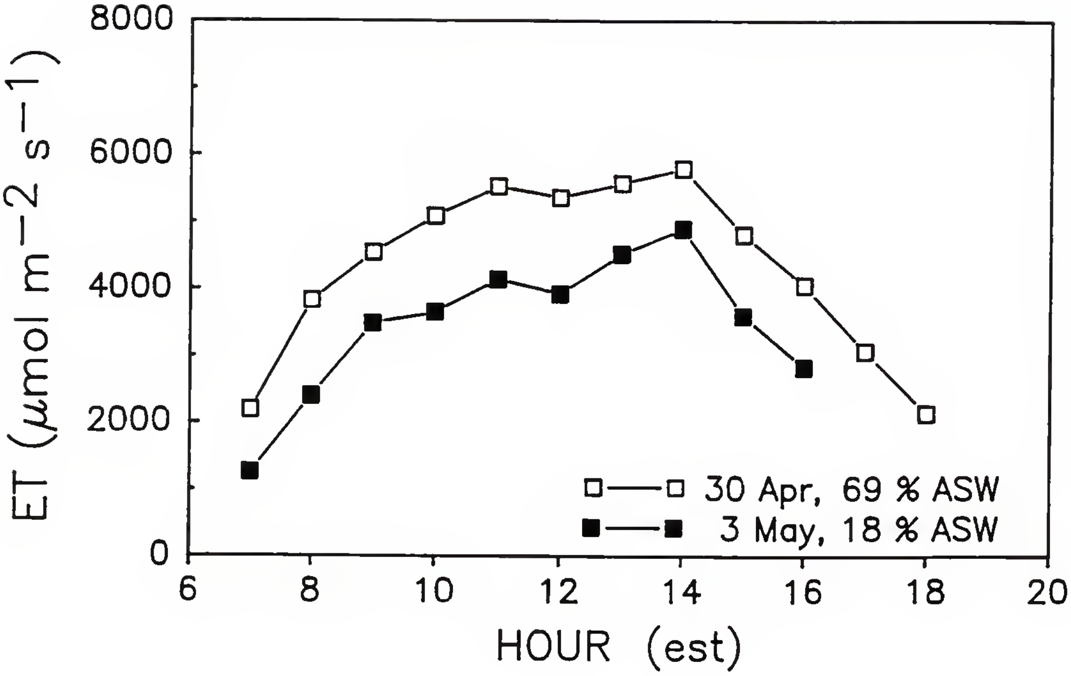


Figure 3.15. Evapotranspiration rates (ET) of Swingle citrumelo citrus seedlings at the intermediate dry-bulb temperature level and elevated CO_2 concentration on days with high (69%) and low (18%) levels of available soil water (ASW).

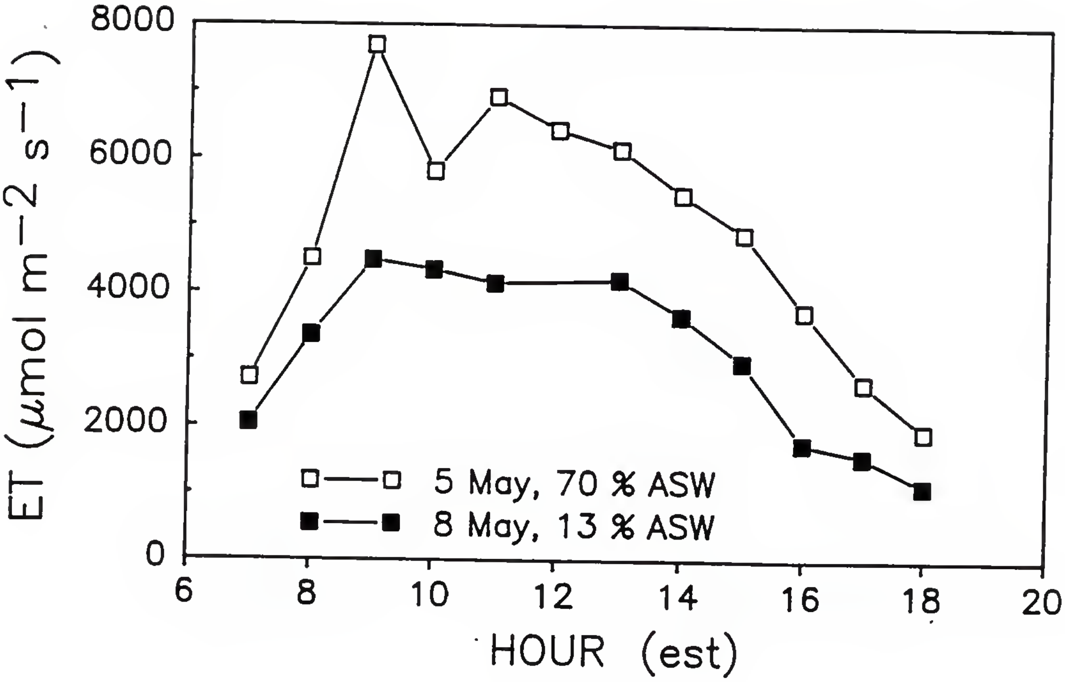


Figure 3.16. Evapotranspiration rates (ET) of Swingle citrumelo citrus seedlings at the high dry-bulb temperature level and elevated CO_2 (840 µmol mol^{-1}) concentration on days with high (70%) and low (13 %) levels of available soil water (ASW).

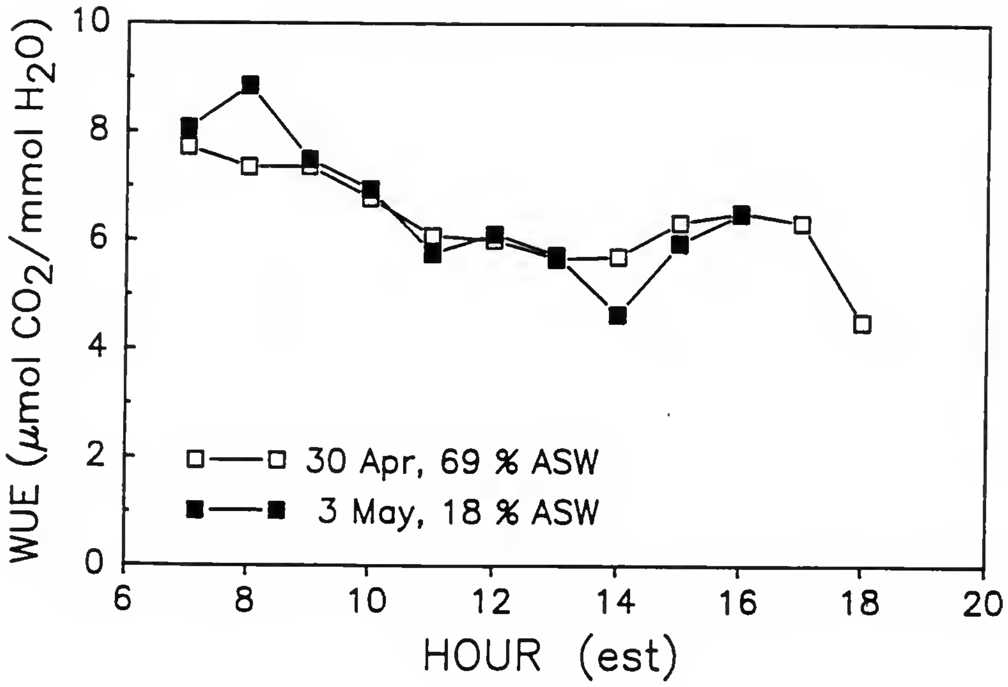


Figure 3.17. Water-use efficiency (WUE) of Swingle citrumelo citrus seedlings at the intermediate dry-bulb temperature level and elevated CO_2 (840 μmol mol^{-1}) concentration on days with high (69%) and low (18%) levels of available soil water (ASW).

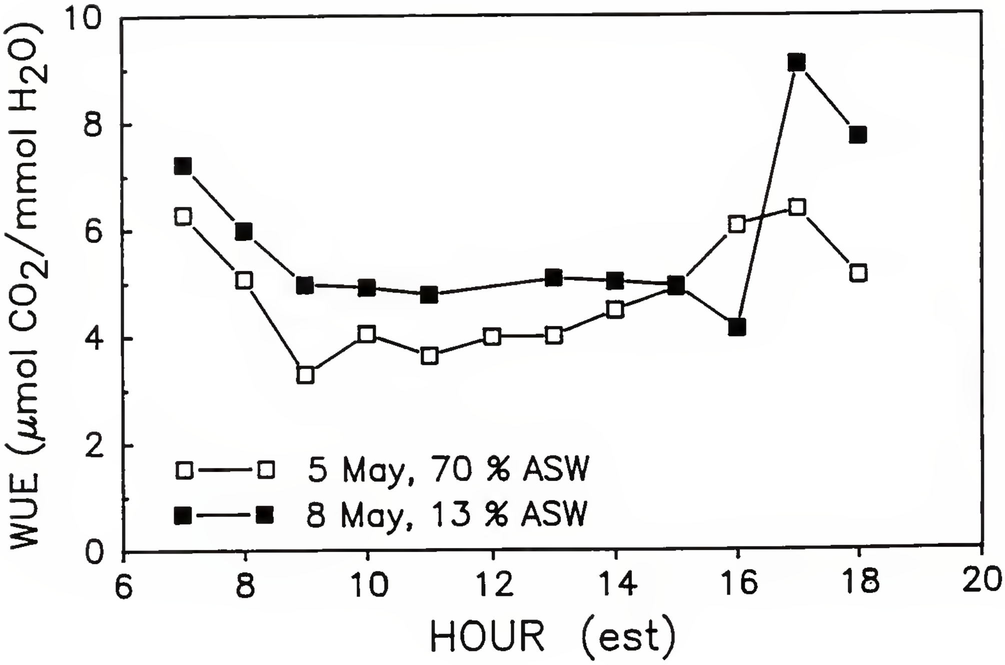


Figure 3.18. Water-use efficiency (WUE) of Swingle citrumelo citrus seedlings at the high dry-bulb temperature and elevated CO_2 (840 µmol mol^{-1}) concentration on days with high (69%) and low (13%) levels of available soil water (ASW).

in Figure 3.19 which shows that maximum CERs remained nearly constant or rose slightly as ASW was depleted from 95 to 7% over a five day period. The slight increase in CERs over this time may represent an increase in leaf area within the chambers. Water stored in plant tissue may represent an important source of water to the plant at this low soil water content. It is expected that if the plants had not been irrigated the evening of the 19 May maximum CERs of the following day would have dropped drastically. At the intermediate DBT/VPD treatment CERs in the early part of the soil drying cycle were limited by low radiation so that the maximum CER of 14.5 occurred at approximately 50% ASW and dropped to 11.0 μmol m^{-2} s^{-1} at 13.5 pecent ASW on the fourth day of the drying cycle (Figure 3.20). At the high DBT/VPD treatment and ambient CO_2 concentration, CERs began to decline when ASW was in the range 60 to 40% and dropped steadily thereafter to 5 μmol m^{-2} s^{-1} at 11% ASW on the fourth day of the drying cycle (Figure 3.21). Thus, it appears that daily maximum CERs were reduced at progressively higher levels of ASW as the DBT/VPD level was increased i.e., the reduction in maximum CER occurred at < 7, between 30 and 50, and between 39 and 64% ASW, at the low, intermediate, and high DBT/VPD levels, respectively.

At the intermediate DBT/VPD level and elevated CO_2 concentration, maximum CERs were in the range 29.5 to 30.9 μmol m^{-2} s^{-1} during the first two days of the soil drying cycle but dropped on the third day to 25.1 μmol m^{-2} s^{-1} (Figure 3.22). The large decrease in CER when ASW was still greater than 50% was not associated with a significant change in radiation rates or other environmental factor. Maximum daily CER remained in the range 24.1 to 26.0 μmol m^{-2} s^{-1} during the next three days

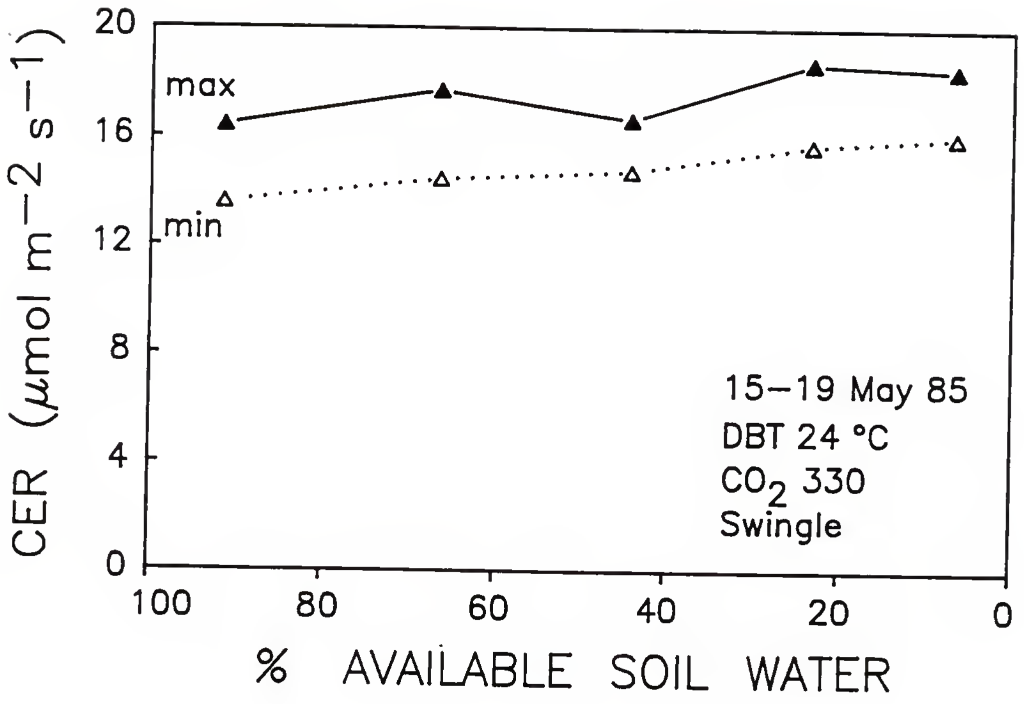


Figure 3.19. Change in diurnal maximum and minimum carbon dioxide exchange rates (CER) of Swingle citrumelo citrus seedlings at the low dry-bulb temperature (DBT) level and ambient CO_2 (330 μmol mol^{-1}) concentration as the available soil water water (%) was depleted.

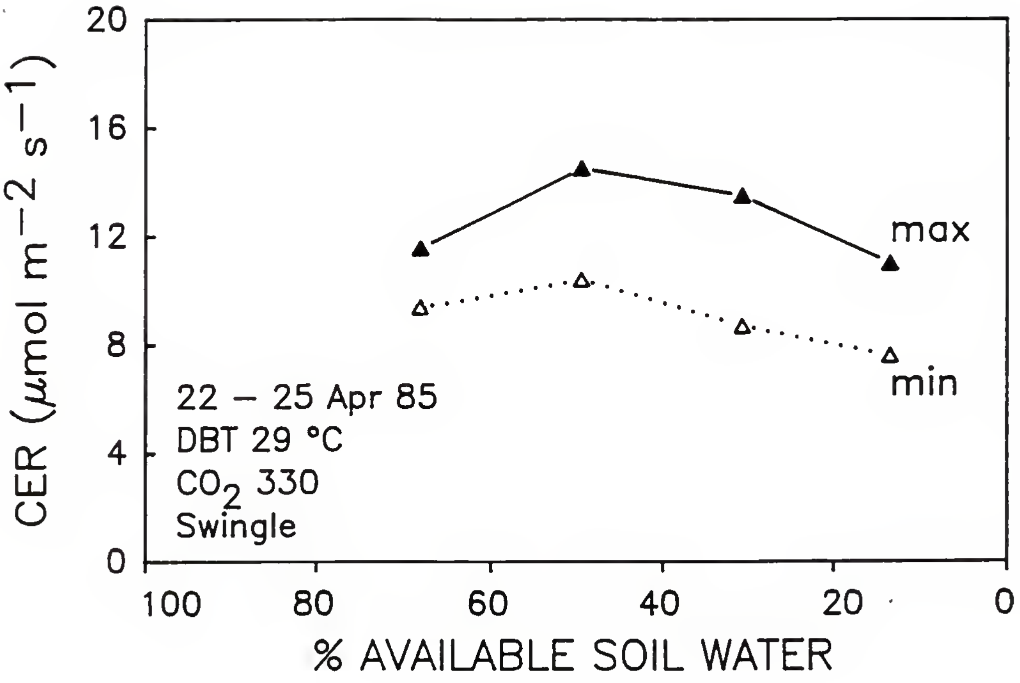


Figure 3.20. Change in the diurnal maximum and minimum carbon dioxide exchange rates (CER) of Swingle citrumelo citrus seedlings at the intermediate dry-bulb temperature (DBT) level and ambient CO_2 (330 μmol mol^{-1}) concentration as the available soil water (%) was depleted.

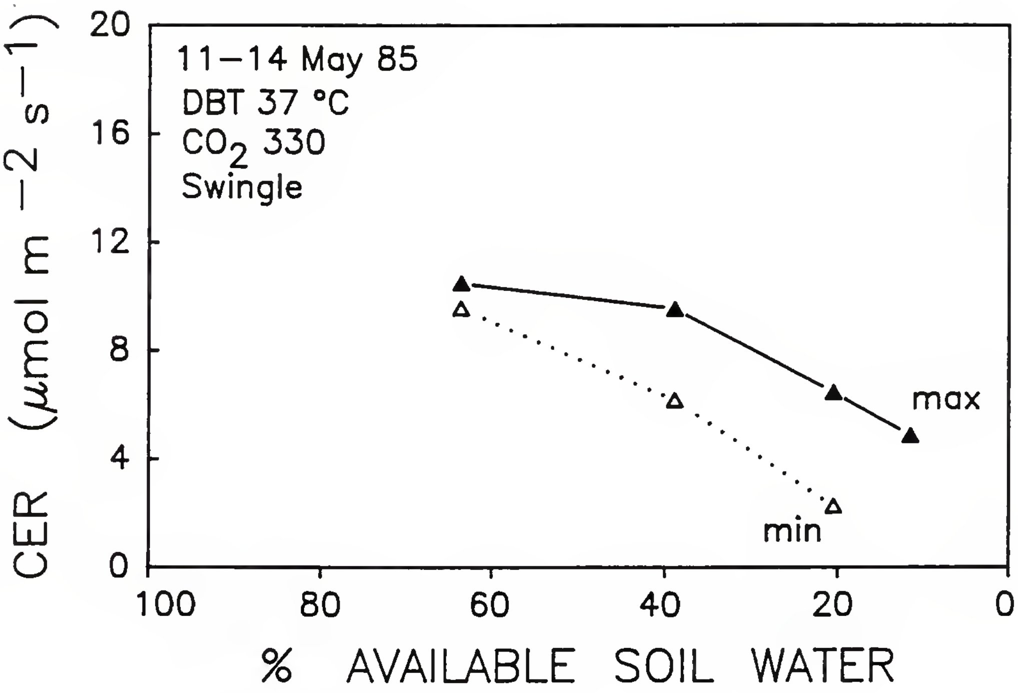


Figure 3.21. Change in the diurnal maximum and minimum carbon dioxide exchange rate of Swingle citrumelo citrus seedlings at the high dry-bulb temperature (DBT) level and ambient CO_2 (330 μmol mol^{-1}) concentration as the available soil water (%) was depleted.

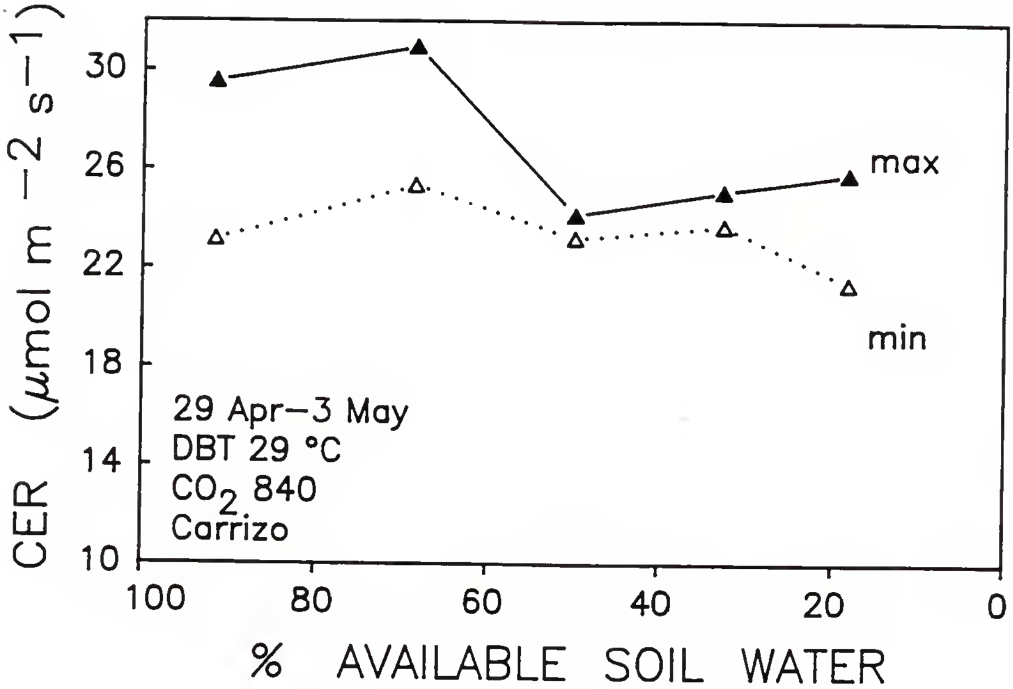


Figure 3.22. Change in the diurnal maximum and minimum carbon dioxide exchange rate (CER) of Swingle citrumelo citrus seedlings at the intermediate dry-bulb temperature (DBT) and elevated CO_2 (840 µmol mol^{-1}) concentration as the available soil water (%) was depleted.

of the soil drying cycle. At 20% ASW there was no indication of further reduction of CERs. When DBT at the elevated CO_2 concentration was raised to 37 °C, daily maximum CERs were nearly constant at approximately 25.0 μmol m^{-2} s^{-1} during the first four days until ASW was depleted to about 30% (Figure 3.23). Maximum CERs dropped to 22.1 μmol m^{-2} s^{-1} at 12% ASW on the fifth day after irrigation and to 20.9 μmol m^{-2} s^{-1} on the sixth day when about 5% of the ASW remained.

Discussion

The results of this study indicate that at the ambient CO_2 concentration the highest CERs were obtained at the low DBT/VPD level and lowest CERs were obtained at the high DBT/VPD level. Low temperature optima have previously been reported for citrus. Kriedemann (1968) found a temperature optimum for orange of 25 °C in humid air and 15 °C in dry air. Khairi and Hall (1976a) reported that maximum leaf photosynthesis of citrus occurred at 22 °C in humid air (0.8 kPa leaf-to-air vapor pressure difference). Photosynthesis was reduced at higher temperatures or greater leaf-to-air vapor pressure differences. Reduction of photosynthesis at higher temperatures was attributed to reductions in mesophyll conductance to CO_2 whereas the effect of increasing vapor pressure deficit was attributed to decreased leaf conductance. In a separate study, Khairi and Hall (1976b) found that net photosynthesis of orange leaves was not reduced at 30 °C and 0.8 kPa VPD when compared to rates obtained at 22 °C and 0.8 kPa. It was proposed that previous growing conditions strongly influenced the temperature optimum. Vu and Yelenosky (1986) found that leaf photosynthetic rates of orange plants

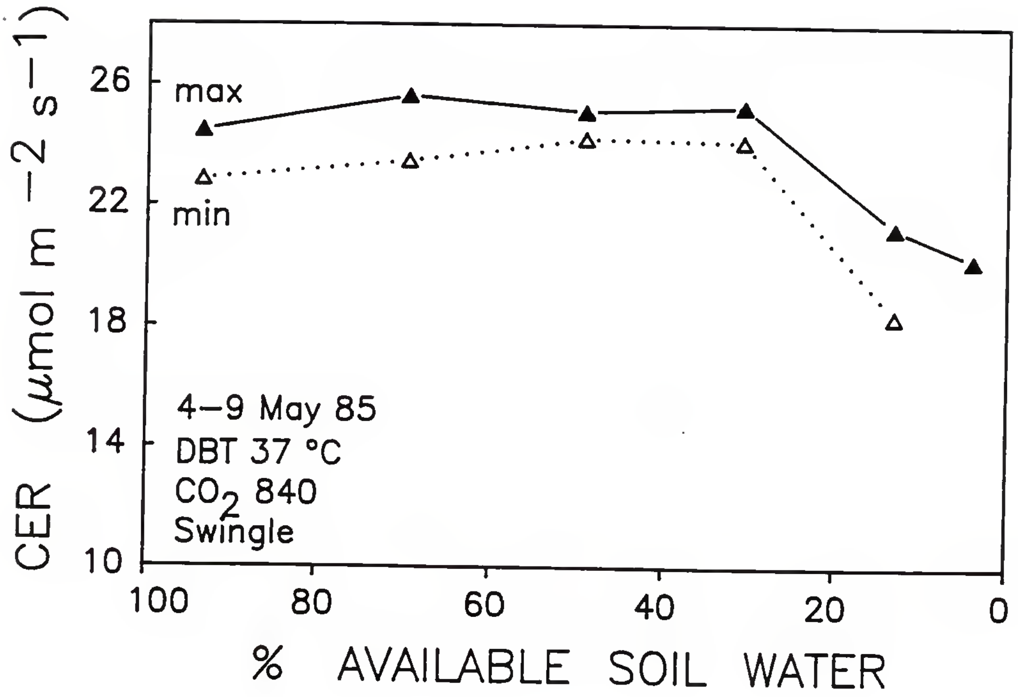


Figure 3.23. Change in the diurnal maximum and minimum carbon dioxide exchange rate (CER) of Swingle citrumelo citrus seedlings at the high dry-bulb temperature (DBT) and elevated CO_2 (840 μmol mol^{-1}) concentration as the available soil water (%) was depleted.

grown at 15.6 °C was 2.15 μmol m^{-2} s^{-1} and increased to 4.51 μmol m^{-2} s^{-1} after 96 hours at 32.2 °C. Both temperatures may represent extremes in the range of optimum temperatures for citrus photosynthesis. In the present study increases in VPD as DBT increased confound the effects of stomatal and nonstomatal factors on CERs. It is evident that stomatal resistance increased as DBT was raised from 24 to 37 °C because maximum ET rates rose only slightly from 7300 μmol m^{-2} s^{-1} at the low temperature to 9000 μmol m^{-2} s^{-1} at the high temperature despite the two-fold increase in VPDs. This type of response of citrus transpiration to increases in humidity deficits has been reported in many other studies and can be attributed to stomatal closure (Halevy, 1956; Hall et al., 1975; Kaufmann and Levy, 1976; Levy, 1980; Sinclair and Allen, 1982). But the role of mesophyll resistance in reduced CERs as the DBT/VPD level increased is less discernible. At this point it is only possible to speculate about it within the range of the observed carbon dioxide exchange rate and transpiration responses. Consideration of soil water status in conjuction with the DBT/VPD level may help in understanding the CER responses to environmental conditions.

Daily maximum and minimum CERs plotted over the percentage ASW throughout various soil water depletion cycles indicated that at both ambient and elevated CO_2 concentrations maximum CER was reduced at progressively higher levels of ASW as both DBT and VPD increased and suggested increasing sensitivity of CERs to soil water depletion as the DBT/VPD level increased. Midday depression of CER was not apparent at any of the DBT/VPD treatments at high soil water levels, but at low soil water contents midday depression was observed at the intermediate and high DBTs. Evapotranspiration was reduced as soil water was depleted but did not show midday depression. These results agree in part with findings of Bielorai and Mendel (1969) that both photosynthesis and transpiration of citrus declined as soil water was depleted but that the effect of reduced soil moisture was greatest on photosynthesis and only photosynthesis showed midday depression at low soil water levels. The authors concluded that at high soil water levels reductions in photosynthesis as DBT increased were primarily due to stomatal closure but low soil water content resulted in increased mesophyll resistance at high temperatures. Thompson et al. (1965) made a similar suggestion when they concluded from their study that high VPD and low soil moisture resulted in increased sensitivity and reduced photosynthesis of citrus leaves at high temperatures. Hoare and Barrs (1974) hypothesized that approximately half of the reduction in net photsynthesis of citrus when subjected to water stress was related to increased mesophyll resistance which increased at the same rate as stomatal resistance.

The results of the present study might be interpreted in a similar manner as were findings from the studies by Bielorai and Mendel (1969) and Thompson et al. (1971). It appears that as DBT/VPD rose there was an increase in transpiration that was limited by stomatal closure that also resulted in reduction of CERs. But as soil water was depleted, or as VPD rose, water stress in the plant may have caused increased mesophyll resistance that was responsible for midday depression of photosynthesis to a greater extent than stomatal closure. It is known that water stress often results in reduction of photosynthesis due to factors other than stomatal closure (Hsiao, 1973). Marler (1988) proposed that increases in internal CO_2 concentrations accompanying reduced stomatal conductance indicated that nonstomatal factors were responsible for reductions in photosynthesis of field grown citrus trees at low soil water levels.

While several studies have discussed the effect of CO_2 enrichment on vegetative growth of citrus (Koch et al, 1983, 1986, 1987), few studies have examined gas exchange responses of citrus at elevated CO_2 concentrations. Downton et al. (1987) noted that photosynthesis of well-watered orange plants at 25 °C were from 18 to 77% greater at 800 μmol mol^{-1} than at 400 μmol mol^{-1} depending on the developmental stage. A doubling of citrus CER at a CO_2 concentration of 840 μmol mol^{-1} is supported by the results of this study. Furthermore, midday depression of CER at the intermediate and high DBT/VPDs when soil water was low was alleviated under elevated CO_2 conditions. It is not possible from this study to determine the mechanism responsible for high CERs at the high DBT, elevated CO_2 concentration, and low soil water content except to speculate that high CO_2 concentrations rendered mesophyll resistance less sensitive to temperature or soil water status.

The results suggest that soil water had the most significant influence of all the environmental variables studied on both CER and transpiration of the citrus seedling canopy. Maximum rates of transpiration in citrus beyond which no further increases in transpiration occur despite increasing evaporative demand have previously been proposed (Sinclair and Allen, 1982). While high sensitivity of citrus stomata to leaf-to-air humidity differences seems to be a feasible explanation, resistances in the root or shoot may be related to induction of leaf water stress and stomatal resistance. High internal resistance to water transport in citrus might also be associated with increased mesophyll resistance at low soil water levels or high evaporative demand and result in reductions in CER. This would suggest that as long as soil water was easily available, midday depression of CER in citrus would not occur.

CHAPTER IV

PARTIAL ROOTING VOLUME IRRIGATION OF YOUNG CITRUS TREES

Introduction

Despite Florida's humid climate and abundant rainfall, an average of more than 1300 mm annually, citrus growers there are increasingly finding themselves, along with growers in such arid environments as Israel, facing an increasing problem of reduced water resources for crop production. Severe freezes in Florida in December 1983 and January 1985 resulted in the loss of about 80,000 ha (200,000 acres) of citrus trees. Largely due to these losses an estimated 6 to 10 million citrus trees were planted annually in Florida during the years 1982 to 1986 (Jackson et al., 1986). At the same time, water management agencies began to institute more restrictive regulations on water use for agricultural purposes. These events promoted widespread installation of micro-irrigation systems in newly established groves as well as conversion of mature groves from conventional, i.e., flood or overhead sprinkler, to micro-irrigation.

Micro-irrigation includes drip, trickle, and microsprayer systems that apply water to limited areas of soil. Irrigation water-use efficiency is improved using micro-irrigation by applying reduced quantities of water, sufficient to meet transpiration requirements, to the volume of soil where roots are concentrated and thereby eliminating excessive percolation below the root zone or evaporation from the soil surface. Irrigation of only a portion of the root system can occur when water applied to a limited area of soil moves predominately vertically with limited lateral distribution. Concern over possible detrimental effects on tree growth when less than the entire root system is irrigated has resulted in many studies of the relative success of conventional and micro-irrigation systems. While many such studies have indicated comparable or improved performance of citrus using micro-irrigation (Aljibury, 1974; Rodney et al., 1977; Bielorai et al., 1981) others have reported variable results (Bielorai, 1977; Moreshet et al., 1983) and in Florida the results have been, nearly unanimously, negative (1974; Koo, 1978: Smajstrla and Koo, 1985; Zekri and Parsons, 1988, 1989).

Evaluation of the relative performance of mature, field-grown, partially-irrigated trees is complicated by difficulties in quantifying the actual portion or volume of roots receiving water and in obtaining reliable estimates of whole-plant photosynthesis, transpiration, water status, and vegetative growth. Various parameters have been used to quantify the irrigated portion of root zone in the field including: percent soil surface area (Bielorai, 1982), root-zone soil volume (Bielorai et al., 1981), relative soil volume per tree (Moreshet et al., 1983), and under-tree canopy area (Koo 1985b). Relative plant performance is typically based on fruit yield. Use of split-root plants in partial irrigation studies permits greater control over the portion of the root system receiving water and has been used to evaluate partial irrigation of apple (Black and West, 1974), peach (Tan and Buttery, 1982) and tomato (Tan et al., 1981). Use of containerized, split-root plants in conjunction with growth chambers permits measurement of whole-plant gas-exchange and growth responses to partial root-volume irrigation but may also be used to evaluate these responses at different levels of climatic conditions. The objectives of this study were: 1) to determine whether reductions in the irrigated root volume caused reductions in gas exchange rates and growth and if so, what portion of the root volume had to be irrigated to avoid significant reductions in growth as compared to fully irrigated trees, 2) to assess gas exchange responses not only with respect to the portion of rooting volume irrigated but also with respect to soil water content and atmospheric conditions to evaluate the capacity of these environmental factors to determine the portion of irrigated rooting volume required, 3) to investigate changes in root hydraulic conductivity as a possible adaptive mechanism of young citrus trees to reduced root-volume irrigation.

Materials and Methods

Preparation of Citrus Trees With Split-Root Systems

In August 1985, one-year old citrus trees with Hamlin scions (*Citrus sinensis*) budded on Carrizo citrange (*Poncirus trifoliata* x *C. sinensis*), sour orange (*C. aurantium*), or Swingle citrumelo (*Poncirus trifoliata* x *C. paradisii*) rootstocks were purchased from a Highlands County, Florida nursery (Hutchinson's Citrus Nursery, Sebring, Florida) and transported to Gainesville. 'Hamlin' is a widely grown juice cultivar. Sour orange is an established rootstock in Florida and Swingle citrumelo and Carrizo citrange are both potentially important rootstocks with growth characteristics well suited to Florida. All plant materials were chosen because of their importance and availability in sufficient quantities at the time the trees were purchased. Roots of the young trees were pruned so that four lateral roots of approximately equal diameter remained as the primary root system. The root-pruned plants were placed in 0.15-m diameter plastic pots with the four lateral roots extending from the pots through four separate holes near the bottom of the pots. Groups of 20 potted plants were grown in shallow trays [0.15 (depth) x 2 (length) x 1 (width) m] with soil covering the lateral roots which extended from the pots.

The trees were grown inside fiberglass greenhouses from August 1985 to February 1986 and hand-irrigated and fertilized at frequent intervals using 20-20-20 N-P_2O_5-K_2O with micronutrients. Water and fertilizer application was directed towards roots growing in the trays, rather than in the pots, to encourage root growth from the four lateral roots. Plants were sprayed with insecticide when needed.

Split-root containers were constructed of galvanized sheet steel. Overall outside dimensions were 0.60 (depth) x 0.40 (length) x 0.15 (width) m and individual compartments measured 0.50 x 0.20 x 0.075 m (Appendix C). The sheet metal walls at the center of the split-root container were cut at an angle so that the 0.15-m diameter plastic pots would be held firmly in place when the seedlings were transferred (Appendix C). Each compartment was fitted with a 0.20 x 0.50 m glass panel to permit observation of root growth. Small drainage ports were built into the outside panel of each compartment situated 0.6 cm above the floor. All seams and glass panels were sealed with silicone caulking material and each compartment was checked for leaks. Dr. William J. Castle, Lake Alfred Citrus Research and Education Center, Florida, provided recommendations for design of the containers. However, the final design was modified to allow up to 12 split-root containers to be placed in each closed environment chamber.

The citrus trees were transferred from the rooting-trays to the split-root containers in February 1986. Only plants with four, nearly equal root masses were used. Roots were pruned to approximately equal masses, estimated visually, if growth was slightly uneven. Each root mass was placed in a separate compartment of the containers which were then filled and hand-packed with washed builders' sand to a depth of approximately 0.45 m, or a soil volume of 6.75 liters in each of the four compartments. Builders' sand was chosen as the growing medium for the following reasons: its textural similarity to the sandiest soils in Florida, it was uniform and relatively free of pests, and, the lack of organic matter in the soil would help to minimize soil respiration in the growth chambers which would interfere with photosynthetic rate measurements. The soil water release curve and calculated hydraulic conductivity for builders' sand are shown in Figures 4.1 and 4.2, respectively. The water release curve and hydraulic conductivity of Astatula fine sand, a soil type on which citrus is commonly grown in Florida, is included for comparison. Quick lime (CaO) at a rate of about 6 kg m^{-3} soil was incorporated into the soil as the containers were

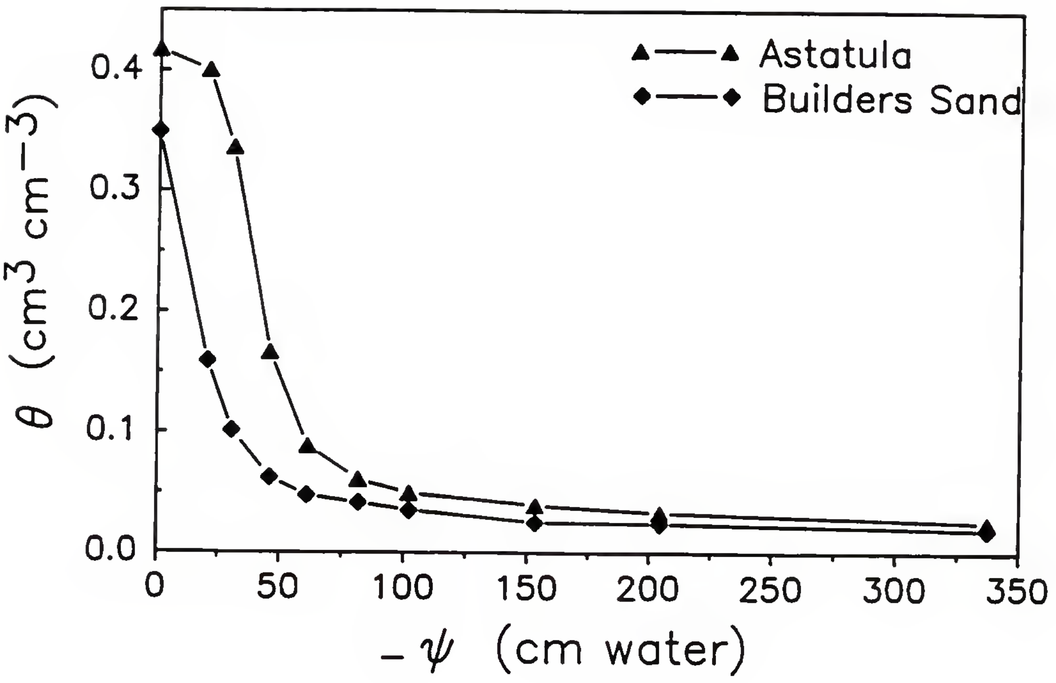


Figure 4.1. Soil water characteristic curve of builders' sand used in the study of partial irrigation of citrus trees and Astatula sand for comparison.

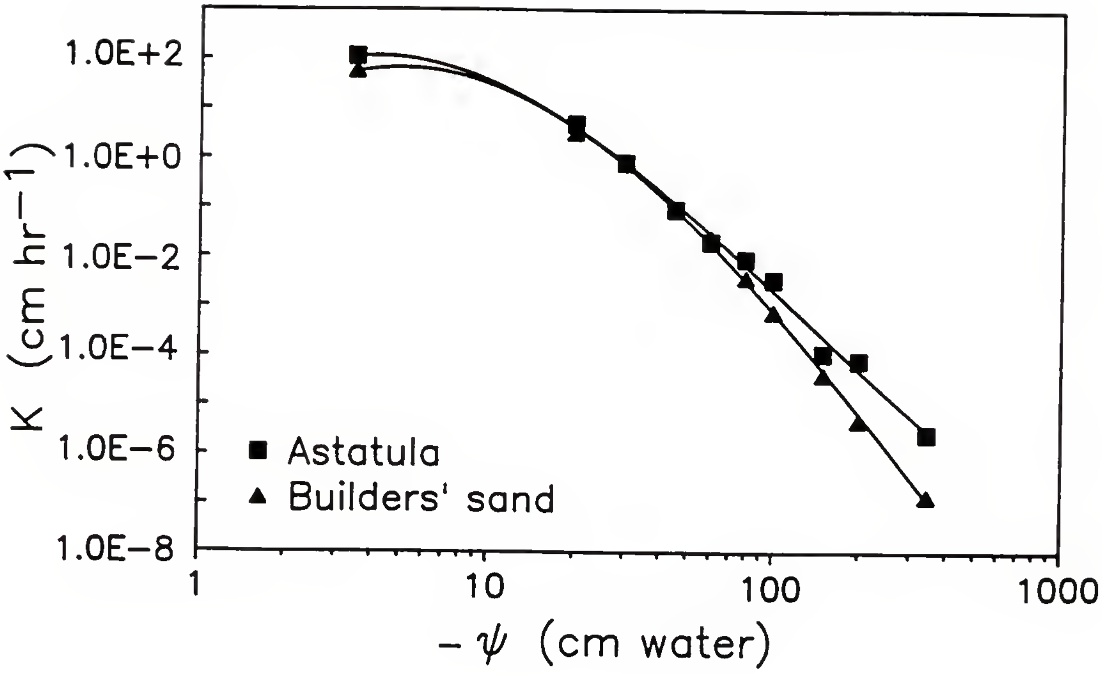


Figure 4.2. Soil hydraulic conductivity of builders' sand used in the partial irrigation of citrus trees study and Astatula sand for comparison.

filled. Plants in the split-root containers were located outside. Plantswere irrigated frequently and fertilized twice weekly with a 20-20-20 N-P_2O_5-K_2O solution with micronutrients, divided equally among the four compartments.

In May 1986, four months after the trees had been transferred to the split-root containers, six plants were sampled for observation of root mass in each of the separate compartments. The percentage of total root dry weight found in a given compartment varied between 22 and 33% of the total. These preliminary measurements indicated that the technique used was satisfactory for obtaining citrus trees with 4 nearly equal, split-root systems.

Experimental Design and Maintenance of Plants in SPAR Chambers

Twenty-one containerized trees were placed in each of six computer-managed, sunlit, controlled-environment growth chambers on 14 June 1986. These chambers, developed at the University of Florida in Gainesville to study plant responses to soil and atmospheric treatments (Jones et al., 1984), were similar to the Soil-Plant-Atmosphere Research units (SPAR units) described by Phene et al. (1978). Three outer walls of the growth chambers were constructed of Mylar polyester film and the top of a rigid plate of cellulose acetate. This portion of the transparent top of the chamber was easily removed for access to the plants. The rigid north wall was constructed of acrylic material and contained exit and entry plenums for ductwork that housed air conditioning equipment (blowers, chilled-water cooling coils, and electrical resistance heaters). The transparent top and walls allowed about 88% of the natural solar photosynthetically active radiation (PAR, 400-700 nm) to enter. Dry-bulb and dew-point temperatures (DBT,DPT, respectively) and carbon dioxide (CO_2) concentration were measured and controlled in the canopy zone. Canopy transpiration rates (ET) were calculated from cooling-coil condensate removal rates, as measured by tipping bucket rain gauges. Canopy carbon dioxide exchange rates (CER) were measured by metering CO_2 to maintain a constant concentration. For this study, CER and ET of each canopy were calculated on the basis of the horizontal area actually occupied by the root system and plant canopy (1.52 m^2) which was estimated to be slightly less than the ground surface area of the chambers (2.0 m^2).

Seven trees on each of the three rootstocks were randomly assigned to one of six chambers (21 trees per chamber). Each chamber was assigned a single irrigation treatment based on the number of compartments of the 4-compartment split-root system that were rewatered on a recurring schedule as soil water content ran low. These treatments were: 1) Fully irrigated or 4/4-Rooting Volume Irrigated (4/4 RVI), 2) 3/4-Rooting Volume Irrigated (3/4 RVI), 3) 1/2-Rooting Volume Irrigated (2/4 RVI), 4) 1/4-Rooting Volume Irrigated (1/4 RVI) or 5) 1/4-Rooting Volume Irrigated plus a soil surface cover of St. Augustine [*Stenotaphrum secundatum* (Walt.) Kuntze] grass (1/4+ RVI). The sixth chamber received a flooding treatment.

The environmental variables measured during this study--DBT, DPT, CO_2 concentration and PAR, were collected throughout the day at 5-minute intervals. Data reported here represent the mean of twelve 5-minute intervals during one hour, e.g. the value reported at 9 EST represents the mean of twelve readings obtained between 9.00 and 9.92 EST. Data points, which occur at each hour, are not indicated on graphs that depict the four irrigation treatments for clarity of treatment differences.

Initial environmental controls were imposed in all chambers simultaneously and included a diurnal DBT curve with a maximum of 29 °C, with a constant DPT of 18 °C. Because of the high radiation input in the chambers and the low water use by the citrus trees the system was unable to maintain the DBT set point of 29 °C so that daily maximum DBT varied between 29 and 33 °C depending on solar radiation levels. This resulted in maximum vapor pressure deficits (VPD) of 2.2 to 3.0 kPa. This combination of DBT and VPD, 29 °C/2.2 kPa, will subsequently be referred to as the low DBT/VPD level. The initial CO_2 concentration in the chambers was 340 μmol^{-1}. During the latter half of the study, short-duration (1 to 2 weeks) variations in DBT and DPT were implemented to record plant response to the irrigation treatments at an increased level of DBT (37 °C) and resultant atmospheric VPD (3.6 kPa). This combination of DBT/VPD, (37 °C/3.6 kPa) will subsequently be referred to as the high DBT/VPD level. Short-term exposures of the plants to an elevated CO_2 concentration (880 μmol^{-1}) were also conducted. Dates of changes in the environmental conditions in the SPAR chambers are listed in Appendix D.

The twenty-one split-root containers were accommodated in 0.61 (depth) x 1.83 (E-W length) x 0.84 (N-S width) m vats situated in the lysimeter portion of each growth chamber. Irrigation was effected by filling the vats with water until the water level was slightly below the soil surface in the containers and then immediately draining the vats.

Drainage ports one cm above the bottom of each compartment were either sealed or left open, which permitted individual compartments to be irrigated by flooding the vats or to remain dry. Initially, the entire rooting volume of each plant was well watered and received water during the first eleven days (14 to 24 June 1986) that plants were in the growth chambers. On 25 June 1986 partial rooting volume irrigation (RVI) treatments were initiated. Irrigation was scheduled on the basis of depletion of plant available soil water (ASW). The total amount of ASW in each chamber was determined by filling and draining the vats in the evening and allowing the excess water to drain out over night; the next morning soil in the containers was considered to be at field capacity. The cumulative daily evapotranspiration (ET) collected as cooling coil condensate beginning that morning until the time when plants were visibly stressed was considered to represent the total plant available soil water in that chamber. Available soil water was calculated by subtracting evening and morning cooling coil condensate for the entire chamber from the total available soil water and thus actually represents the average ASW of all the irrigated rooting compartments in a chamber. Use of this method for determining soil water status was necessitated by the inability to obtain soil water potential readings on the coarse soil with tensiometers, and also because the small volume of soil in each rooting compartment of the split-root containers prevented use of a gravimetric technique. Irrigation was scheduled when the calculated ASW was approximately two-thirds depleted. This method of irrigation scheduling resulted in an irrigation frequency that averaged 3 times per week for plants with only 1/4 of their rooting volume wetted and once every 6-7 days for fully irrigated plants of the 4/4 RVI treatment. This management scheme was representative of 'periodic' low volume irrigation management rather than 'continuous' or 'high frequency' trickle irrigation.

Plants were irrigated regularly with a commercial water-soluble fertilizer and sprayed intermittently with a foliar micronutrient solution. Fertilization frequency was greater for plants with partial rooting volume wetting than for fully-irrigated plants so as to compensate for the reduced soil volume and thus soil nutrient availability. All soils were 'flushed' at approximately three-week intervals to prevent harmful salt build-up. Samples of the soil solution in each treatment were taken three times during the study and analyzed for pH levels. At all times the soil solution pH was in the range 6.0 to 7.0, an acceptable range for young citrus trees.

Plant water status throughout the course of several soil drying cycles was measured using a Li-Cor Model 1600 steady-state porometer to determine leaf stomatal resistance and a Scholander pressure chamber for determination of leaf xylem water potential. Midmorning and midafternoon stomatal resistances were measured on the abaxial surface of three upper, recently expanded leaves of separate plants on each rootstock (9 leaves total per treatment). Midafternoon leaf xylem potential was measured similarly.

Harvest Procedures

Measurement of root hydraulic conductivity

Sampling of trees for measurement of plant biomass and root hydraulic conductivity began on 15 September 1986. Single trees from each chamber were harvested consecutively and 3 to 4 trees were harvested per day so that at any time during the 28-day period of harvest there was an approximately equal number of trees remaining in each controlled environment growth chamber.

Trees were removed from the split-root container by washing out the soil with a gentle stream of water and carefully lifting out the roots to prevent breakage. Each of the lateral roots from separate compartments was marked with a colored tag to identify root masses from an irrigated or nonirrigated compartment. The center plastic pot was then snipped off and the soil washed away. In all instances, feeder roots in the center pot appeared dehydrated and dead. Each bare-root tree was photographed and placed in a container with its root system immersed in tap water. The tree was carried into the lab and allowed to adjust to conditions of low light and room temperature for 20 minutes before measurements were initiated.

Roots masses in each of the 4 compartments were detached from the plant near the point where the laterals joined the truncated taproot at their base. In the case of very extensive root systems, a single sublateral root was selected for measurement of hydraulic conductivity. The root was placed in the water-filled chamber of a Scholander pressure bomb and the cut end of the root was fitted with a piece of Tygon tubing which was then filled with water. Root exudate was collected in a covered beaker. Placement of roots in the chambers required less than 5 minutes. Pressure within the chamber was increased at a rate of approximately 0.05 MPa s^{-1} up to 0.4 MPa. Following an initial equilibration period of 15 minutes the roots remained in the chambers at 0.4 ± 0.05 MPa for a period of one hour during which exudate was collected. Four pressure chambers were used so that hydraulic conductivity could be measured simultaneously on all 4 root masses of a single plant. Six trees from each treatment (2 of each rootstock) were used for root conductivity measurements.

Upon removal of roots from the pressure chambers the diameter of the cut end was recorded. A subsample from each root mass which consisted of approximately 1/4 to 1/3 of the total root mass was separated into nonfeeder roots (diameter $\geq$ 1.5 mm, by visual estimation) and feeder roots (diameter < 1.5 mm, by estimation). Separated roots were placed on moist paper towels and misted frequently to prevent drying and shrinkage of roots. These 'subsample' roots were placed through a Li-Cor Model 3000 leaf area meter for measurement of two-dimensional surface area. Correlation of the surface areas of small segments of wire calculated from width and length measurements to the area meter values showed a close relation between the two measurements. Roots were carefully placed on the meter belt to avoid excessive overlapping. Length of subsample roots was estimated using the line-intersect method described by Tennant (1975) with 10 x 10 mm grid squares.

Area, but not length, of the remaining portion of roots used for conductivity measurement was determined in the manner described above after separating roots into nonfeeder and feeder categories. Roots of the subsample, sample, and any unsampled portions of the roots (i.e., in) the case of very large root systems, the portion not placed in the pressure chamber) were dried separately in an oven at 70 °C for 24 hours and then weighed.

Measurement of biomass

Shoots of the trees were separated into new and old leaves and new and old shoots; leaf area was measured using the area meter. Because the point of shoot extension of citrus is very distinct for recent flushes of growth, it was possible to distinguish older leaves and shoots from more recent (3-month old) growth with considerable certainty. Shoots and leaves were dried at 70 °C for 48 hours and weighed. Another 9 trees from each chamber were sampled for biomass measurements only; this included leaf area and leaf and shoot dry weights as described above. Roots were separated into feeder and nonfeeder categories and dry weights were recorded.

Statistical Procedures

Because of the lack of replication of partial rooting volume irrigation treatments regression was used to determine relationships between new leaf area, dry weights of new leaves and stems, root hydraulic conductivity, and the fraction of rooting volume irrigated. Simple linear regression was used for the first attempt of data analysis and found to provide a good fit to the data. Differences in biomass accumulation between rootstock cultivars within each irrigation level were determined using analysis of variance and Duncan's Multiple Range

Test for separation of means. All statistical analyses were performed with the Statistical Analysis System (SAS).

Results

Effect of Atmospheric Variables on Diurnal Gas Exchange

Diurnal patterns of carbon dioxide exchange rate, ET and WUE responses of the citrus trees as influenced by the environmental factors of DBT/VPD and CO_2 concentration were distinct regardless of the level of partial irrigation. Therefore, to simplify the discussion of DBT/VPD, CO_2 concentration and ASW effects on the gas exchange responses of citrus trees at various levels of irrigation, the general diurnal gas exchange patterns are discussed initially. The graphs in this section represent data obtained from the fully irrigated treatment (4/4 RVI) on days with high photosynthetically active radiation (PAR) and plant available soil water (ASW) levels. Differences in gas exchange responses due to partial irrigation treatments are presented and discussed subsequently. Because of the large amount of data collected and the general consistency of treatment differences throughout the study, data from 1 August, when ASW levels in all treatments were similar, are representative of treatment differences and are presented in this part. It is important to note that the percent ASW indicated on the plots represents levels at 0700 eastern standard time (EST) but that it was possible for a considerable percentage of ASW to be lost by the end of the day (1900 EST).

Low DBT/VPD, ambient CO_2 conditions

Photosynthetic carbon dioxide exchange rates at the low DBT/VPD level and ambient CO_2 concentration, are represented by data obtained on 30 July 1986. Diurnal PAR, VPD, DBT, and DPT curves for the 4/4 RVI treatment on this day are shown in Figure 4.3. Data points represent the average of the 12 5-minute interval readings during the indicated hour. Available soil water at 0700 EST was 81%. Each one-hour mean value is plotted at the beginning of the hour. Diurnal gas exchange data are plotted in Figure 4.4. Maximum canopy CERs on this day, as was typical under these conditions, were reached between 0800 and 1100 EST and were on the order of 4 to 8 μmol m^{-2} s^{-1} during the early part of the study and rose to 8 to 13 μmol m^{-2} s^{-1} by the end of the study. The increase in CERs over the season is attributed to an increase in leaf area within each chamber that was detectable visually but was not measured. The reduction in CERs in comparison to those obtained in the 1985 study is likely due to the smaller plant canopy in the chambers in 1986. Carbon dioxide exchange rates typically began to decline between 0900 and 1100 EST and reached a daily minimum between 1200 and 1400 EST when radiation levels reached a maximum. On some days there was an increase in CERs between 1400 and 1700 EST.

Carbon dioxide exchange rate data from 10 August plotted over radiation levels exhibits hysteresis and suggests that other, diurnally changing variables influenced CERs (Figure 4.5). Figure 4.3 shows that the typical, diurnal change in VPD was similar to that of PAR. Vapor pressure deficits increased from a value slightly greater than 1.0 kPa in the early morning to 2.5 kPa for most treatments by 1100 EST.

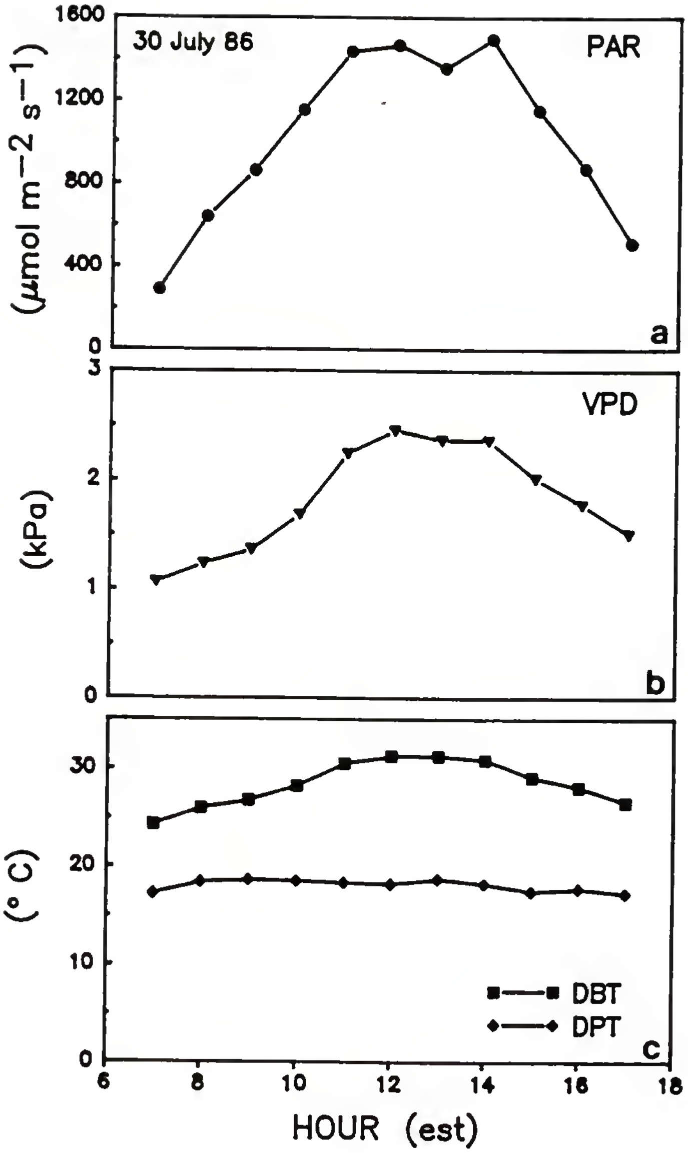


Figure 4.3. Environmental conditions in the growth chamber for fully irrigated (4/4 RVI) citrus trees at ambient CO_2 (340 µmol mol^{-1}) and 81% available soil water on 30 July 1986:
a) Photosynthetically active radiation (PAR),
b) Atmospheric water vapor pressure deficit (VPD),
c) Dry-bulb and dewpoint temperatures (DBT and DPT, respectively).

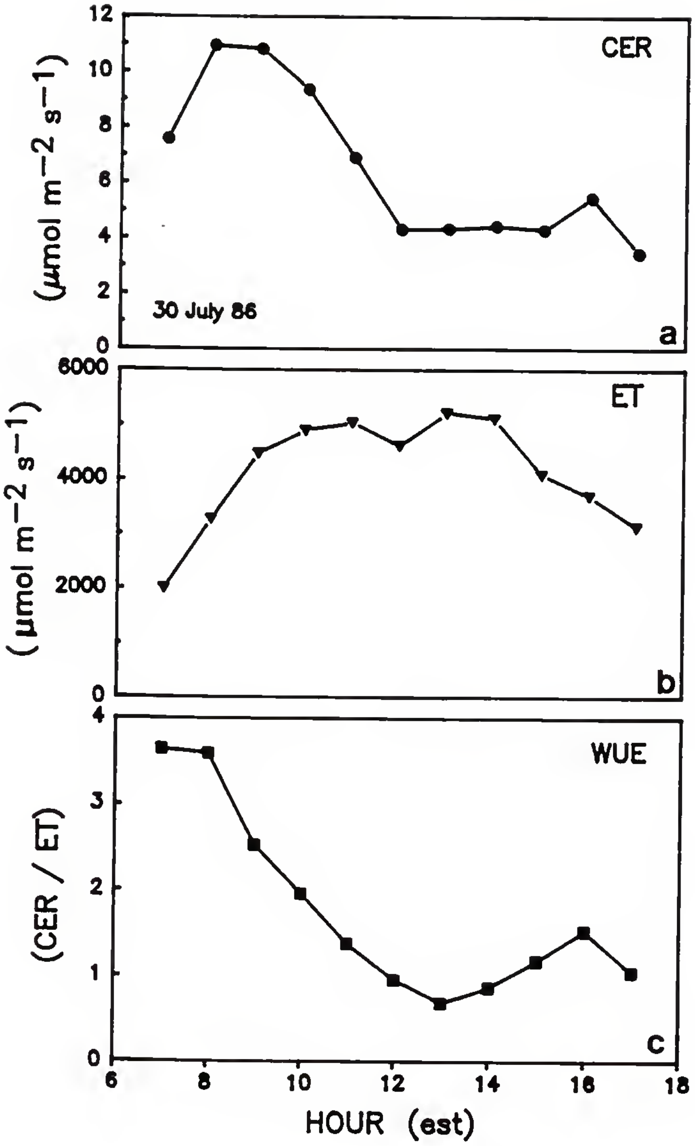


Figure 4.4. Gas exchange responses of fully irrigated (4/4 RVI) citrus trees on 30 July 1986:
a) Photosynthetic carbon dioxide exchange rate (CER),
b) Evapotranspiration (ET),
c) Water-use efficiency (WUE, μmol CO_2/mmol H_2O).

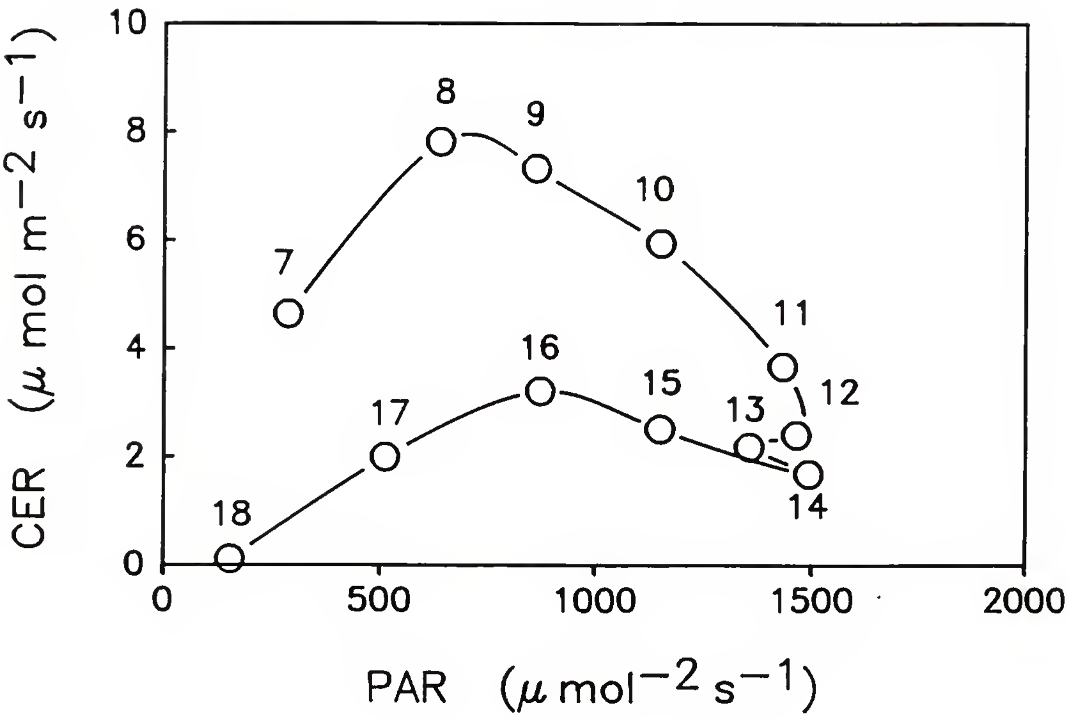


Figure 4.5. Carbon dioxide exchange rate (CER) vs. photosynthetically active radiation (PAR) of fully irrigated (4/4 RVI) citrus trees on 10 August 1986. Numbers above the data points indicate the hour of day during which the measurements were made.

Variation in VPDs throughout the day was largely due to an increase in DBT resulting from increasing solar radiation levels during the day. Carbon dioxide exchange rates plotted over VPD show the same type of hysteresis as that observed in the light response curve and suggest interactive effects of PAR and DBT/VPD conditions on CER (Figure 4.6).

The typical diurnal pattern of ET at the low DBT/VPD level and ambient CO_2 concentrations, represented by data from 30 July 1986 (Figure 4.4), paralleled the diurnal PAR curve. Evapotranspiration rose between 0700 and 0900 EST and thereafter remained nearly constant in the range of 4500 to 5200 μmol (H_2O) m^{-2} s^{-1} until radiation levels began to decline.

The diurnal pattern of CER combined with that of ET rates resulted in WUE values that were greatest during the early morning hours (0800 to 1000 EST) and declined steadily thereafter reaching a minimum during the middle of the day (Figure 4.4). On days when CERs recovered during the latter hours of the afternoon, WUE also increased during the same period. Data from 30 July 1986 show that maximum WUE was usually less than 4 μmol (CO_2) mmol^{-1} (H_2O), and as low as 1 μmol (CO_2) mmol^{-1} (H_2O) in the early afternoon.

The high DBT/VPD, ambient CO_2 conditions

Although daytime temperature controls were in effect between 0600 and 2000 EST throughout the study, the cooling system was unable to maintain the low DBT control setpoint of 29 °C during the day due to rising solar radiation levels and the increased heat load within the chambers. Thus, at the low DBT/VPD level, DBT within the chambers

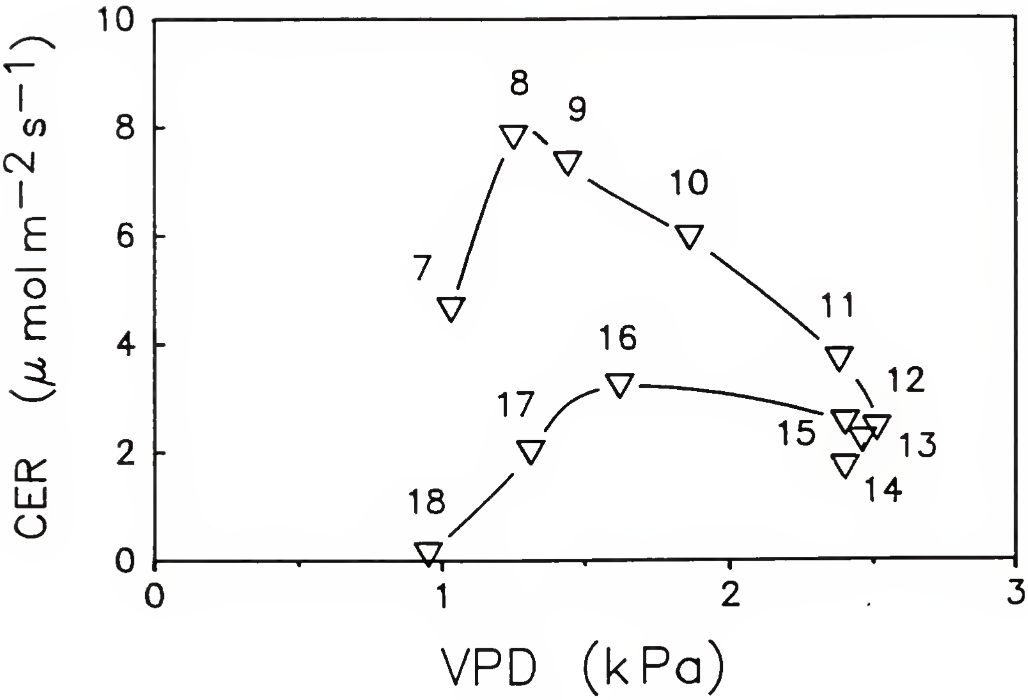


Figure 4.6. Carbon dioxide exchange rate (CER) vs. vapor pressure deficit (VPD) of fully irrigated (4/4 RVI) citrus trees on 10 August 1986. Numbers above the data points indicate the hour of day during which the measurements were made.

increased as the radiation level increased, resulting in a diurnal pattern of VPD that followed the diurnal radiation curve. From 04 to 11 August 1986, DBT/DPT controls were increased to 37 °C and 22 °C, respectively, at ambient CO_2 concentrations. During this period VPDs were from 1.0 to 2.5 kPa greater between 1100 and 1400 than at the low DBT/DPT level and, because temperature control was facilitated, VPDs were more constant throughout the day.

Environmental data from 8 August 1986 are shown in Figure 4.7 and represent conditions during the period of high DBT/VPD for the 4/4 RVI treatment. Gas exchange data from 8 August 1986 on this day when ASW was 95% are shown in Figure 4.8. Maximum CERs were reduced from 10 to 12 μmol m^{-2} s^{-1} at low temperatures to less than 8 μmol m^{-2} s^{-1} during this period of high DBT/VPD and rather than following the previous diurnal pattern with a morning peak before 1100 EST and midday depression, CERs reached a maximum before 1000 EST. The high DBT/VPDs level resulted in lower, but more constant CERs during the day.

Evapotranspiration rates under the elevated DBT/VPD conditions were typically in the range 5000 to 6500 mmol m^{-2} s^{-1} between 1000 and 1400 EST when radiation levels were high and nearly constant. This is only a slight increase in ET over the rates obtained at the low DBT/VPD level and implies strong stomatal control on water loss. Water use efficiency was reduced from a morning maximum of 4 μmol (CO_2) $mmol^{-1}$ (H_2O) under the low DBT/VPD conditions (Figure 4.4) to less than 2 μmol (CO_2) $mmol^{-1}$ (H_2O) under the elevated DBT/VPD conditions (Figure 4.8). Afternoon recovery of WUE was not evident under these conditions on 8 August 1986 because solar radiation decreased rapidly at 1500 EST.

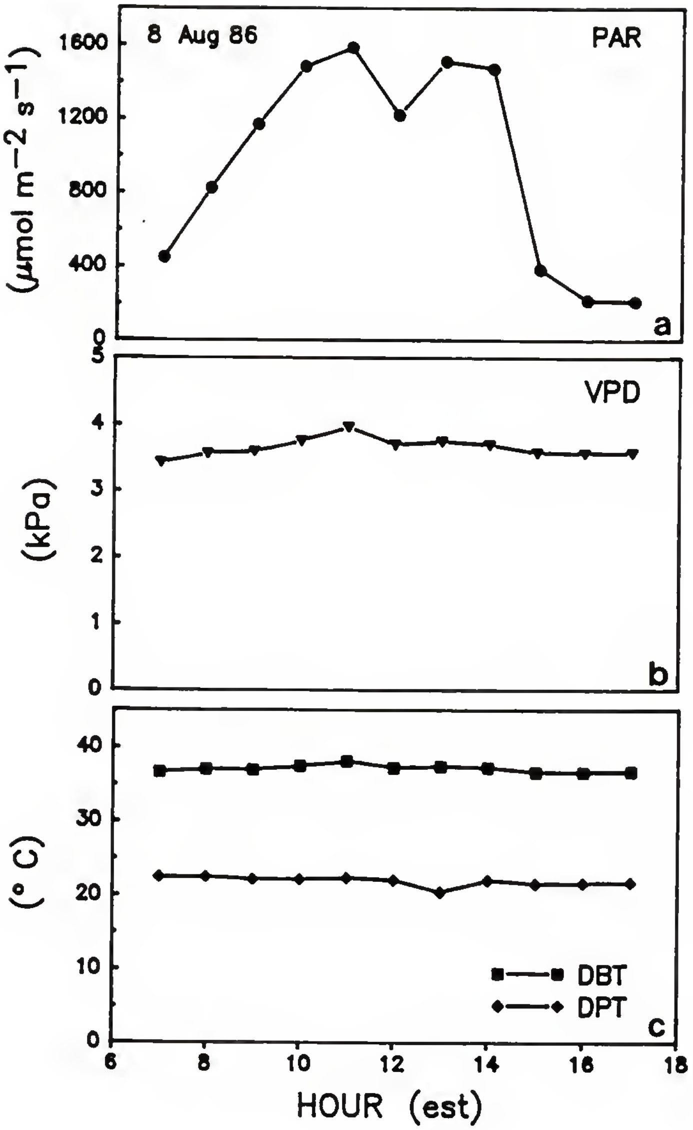


Figure 4.7. Environmental conditions in the chamber for fully irrigated (4/4 RVI) citrus trees at ambient CO_2 concentration (340 μmol mol^{-1}) and 95% available soil water on 8 August 1986:
a) Photosynthetically active radiation (PAR),
b) Atmospheric water vapor pressure deficit (VPD)
c) Dry-bulb and dewpoint temperatures (DBT and DPT, respectively)

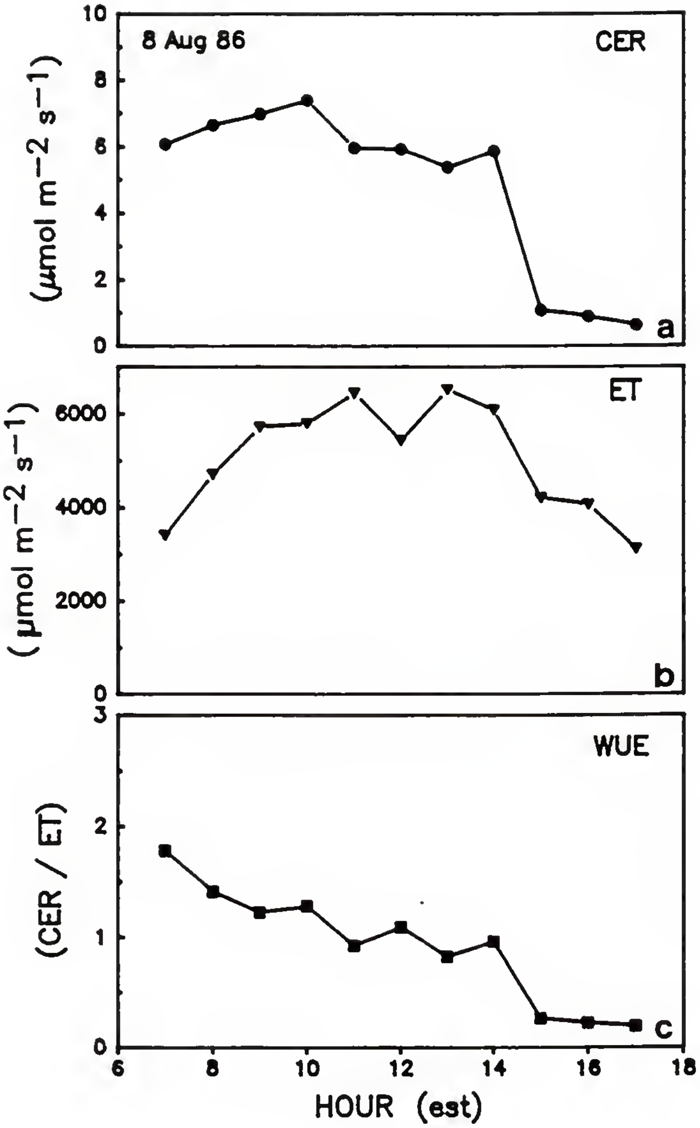


Figure 4.8. Gas exchange responses of fully irrigated (4/4 RVI) citrus trees on 8 August 1986:
a) Photosynthetic carbon dioxide exchange rate (CER),
b) Evapotranspiration (ET),
c) Water-use efficiency (WUE, µmol CO_2/mmol H_2O).

High DBT/VPD, elevated CO_2 conditions

Between 11 and 20 August, CO_2 concentration in the chambers was increased to 880 μmol^{-1} at the high DBT level. Representative data from this period were taken from 17 August 1986. Environmental conditions are shown in Figure 4.9 and gas exchange data in Figure 4.10 for the 4/4 RVI treatment. During this period, maximum mid-morning CERs were double those obtained under ambient CO_2 conditions and high DBT, and ranged from 15 to 29 $\mu mol\ m^{-2}\ s^{-1}$. Generally, midday depression of CERs was less severe, even when the soil water level was low and VPDs were greater than 2.0 kPa. At elevated CO_2 concentrations ET rates between 1000 and 1400 EST ranged from 4500 to 6000 $mmol\ m^{-2}\ s^{-1}$, approximately equal to rates that occurred at the ambient CO_2 level. Maximum WUE ranged from 6 to 8 $\mu mol\ (CO_2)\ mmol^{-1}\ H_2O$, more than twice that obtained at ambient levels.

Low DBT/VPD, elevated CO_2 conditions

When DBT was switched to the low control level of 29 °C at the elevated CO_2 concentration (Figure 4.11), maximum CERs rose to 35 $\mu mol\ m^{-2}\ s^{-1}$ compared to 15 to 29 $\mu mol\ m^{-2}\ s^{-1}$ at the high DBT/VPD level and elevated CO_2 concentration. Evapotranspiration remained in the range 5000 to 6000 $mmol\ m^{-2}\ s^{-1}$ between 1000 and 1400 EST and WUE was in the range of 11 to 5 throughout the day (Figure 4.12). Data shown for 25 August are representative of responses recorded under these conditions.

Effect of Soil Water Level on Photosynthesis and Transpiration

The general effect of soil water depletion on CERs under the different levels of DBT/VPD and CO_2 concentration can be discerned by

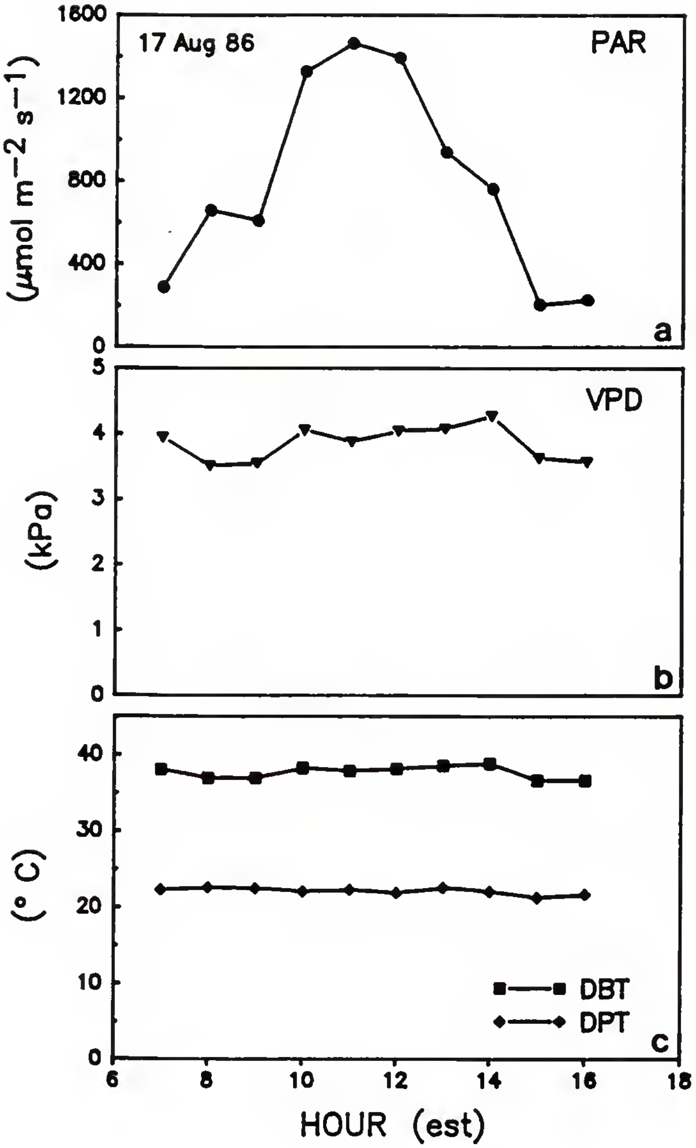


Figure 4.9. Environmental conditions in the chamber for fully irrigated (4/4 RVI) citrus trees at elevated CO_2 concentration (880 µmol mol^{-1}) and 100% available soil water on 17 August 1986:
a) Photosynthetically active radiation (PAR),
b) Atmospheric water vapor pressure deficit (VPD),
c) Dry-bulb and dewpoint temperatures (DBT and DPT, respectively).

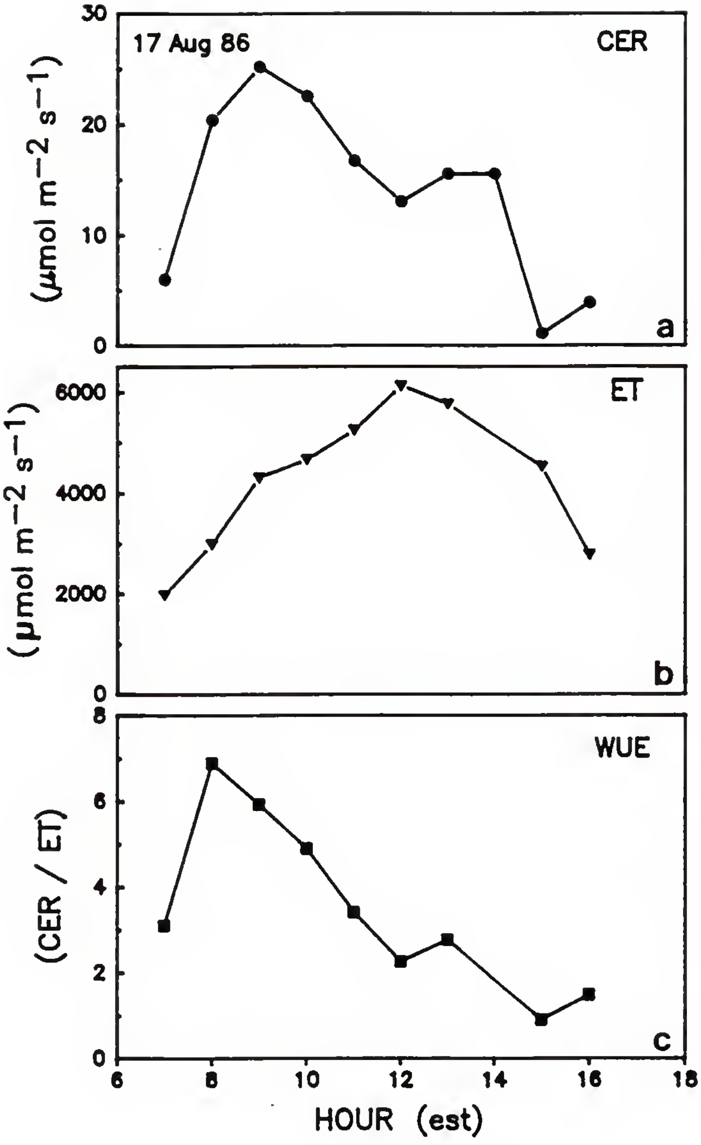


Figure 4.10. Gas exchange responses of fully irrigated (4/4 RVI) citrus trees on 17 August 1986:
a) Photosynthetic carbon dioxide exchange rate (CER),
b) Evapotranspiration (ET),
c) Water-use efficiency (WUE, μmol CO_2/mmol H_2O).

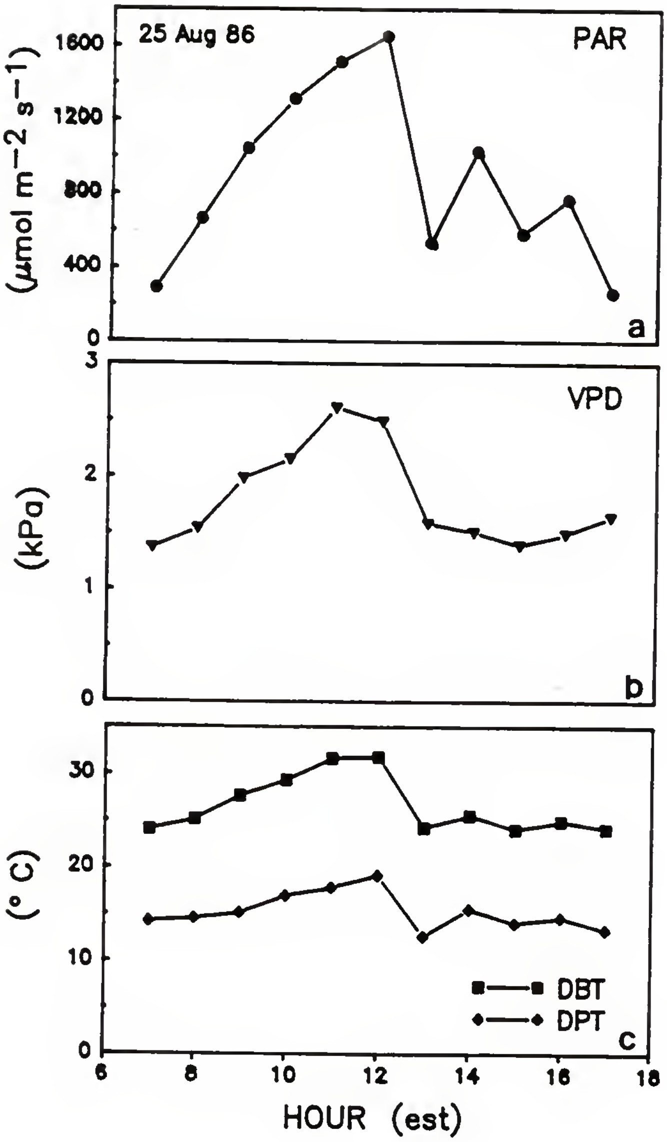


Figure 4.11. Environmental conditions in the chamber for fully irrigated (4/4 RVI) citrus trees at elevated CO_2 concentration (880 μmol mol^{-1}) and 80% available soil water on 25 August 1986:

a) Photosynthetically active radiation (PAR),
b) Atmospheric water vapor pressure deficit (VPD),
c) Dry-bulb and dewpoint temperatures (DBT and DPT, respectively).

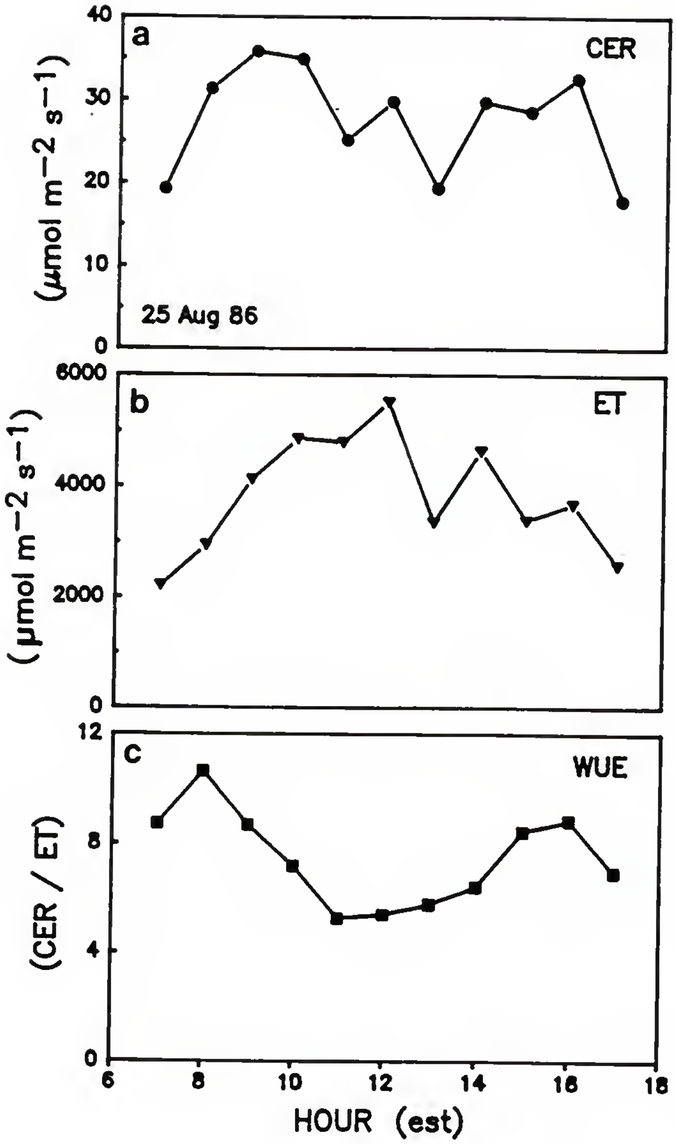


Figure 4.12. Gas exchange responses of fully irrigated (1/4 RVI) citrus trees on 25 August 1986:

a) Photosynthetic carbon dioxide exchange rate (CER),

b) Evapotranspiration (ET),

c) Water-use efficiency (WUE, µmol CO_2/mmol H_2O).

examining the diurnal CER patterns on separate days at high and low ASW levels. Data presented here are again from the 4/4 RVI treatment. The effect of soil drying was most evident on early morning CERs. At the low DBT/VPD, ambient CO_2 concentration level, CERs were reduced throughout the day as ASW was reduced (Figure 4.13). Maximum morning CER was reduced from 9 to 6 μmol m^{-2} s^{-1} at ASW levels of 92 and 57% on 28 June and 2 July, respectively, but because of the depressed CERs on both dates midafternoon CER was reduced only slightly in comparison. Midafternoon recovery of CER was not apparent on days with low ASW. Under the high DBT/VPD conditions later in the study on 8 and 10 August, morning CERs were similar at the high and low ASW level but midafternoon CERs were reduced as soil water was depleted (Figure 4.14).

As is indicated in Figure 4.15, the effect of soil water depletion on photosynthetic CER was apparent at relatively high levels of ASW. Relatively small reductions in soil water content below the level of saturation resulted in severe reductions in CER. This drastic effect is likely due to the high porosity of builder's sand and consequent low hydraulic conductivity even at relatively high volumetric water contents. Water present in the soil therefore was not necessarily available to plant roots.

At low DBT/VPD level and elevated CO_2 concentration, maximum midmorning CERs were greater than 25 μmol m^{-2} s^{-1} at high levels of ASW (21 August) and were reduced to 20 μmol m^{-2} s^{-1} when ASW was reduced to 35% (23 August, Figure 4.16). Under these conditions midday depression of CERs was evident when ASW was reduced, but was not as severe as under ambient CO_2 conditions (Figure 4.14). At the high DBT/VPD level and

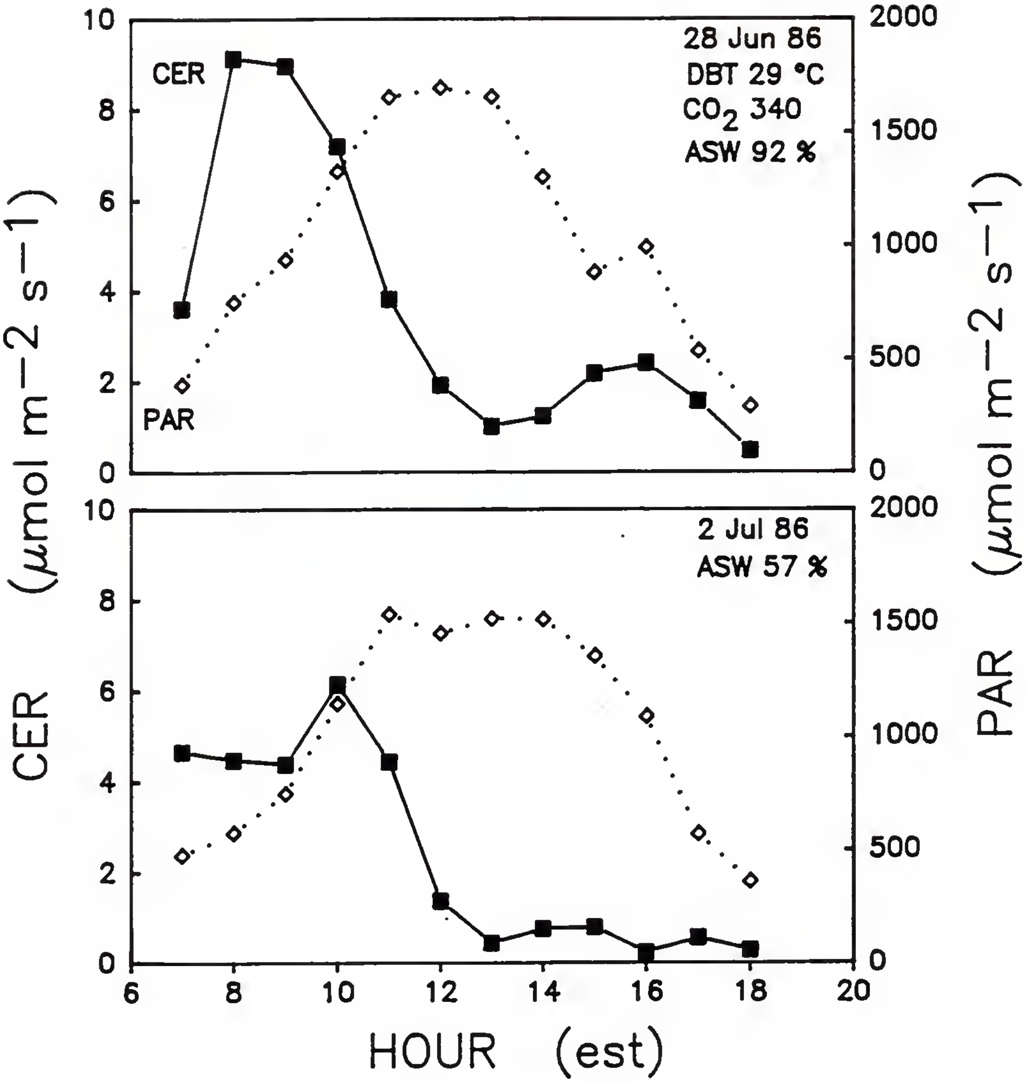


Figure 4.13. Carbon dioxide exchange rates (CER) of fully irrigated (4/4 RVI) citrus trees and photosynthetically active radiation (PAR) at the low dry-bulb (DBT) and ambient CO_2 concentration on days with high (92%) and low (57%) levels of available soil water (ASW).

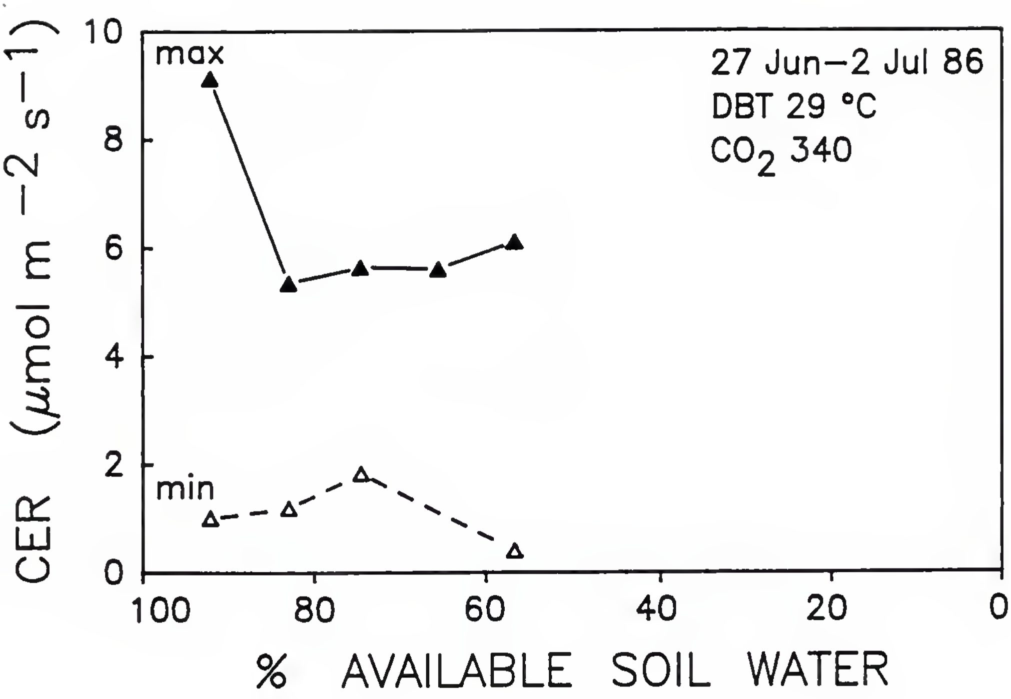


Figure 4.14. Reduction in diurnal maximum and minimum carbon dioxide exchange rates (CER) of fully irrigated (4/4 RVI) citrus trees as available soil water was depleted.

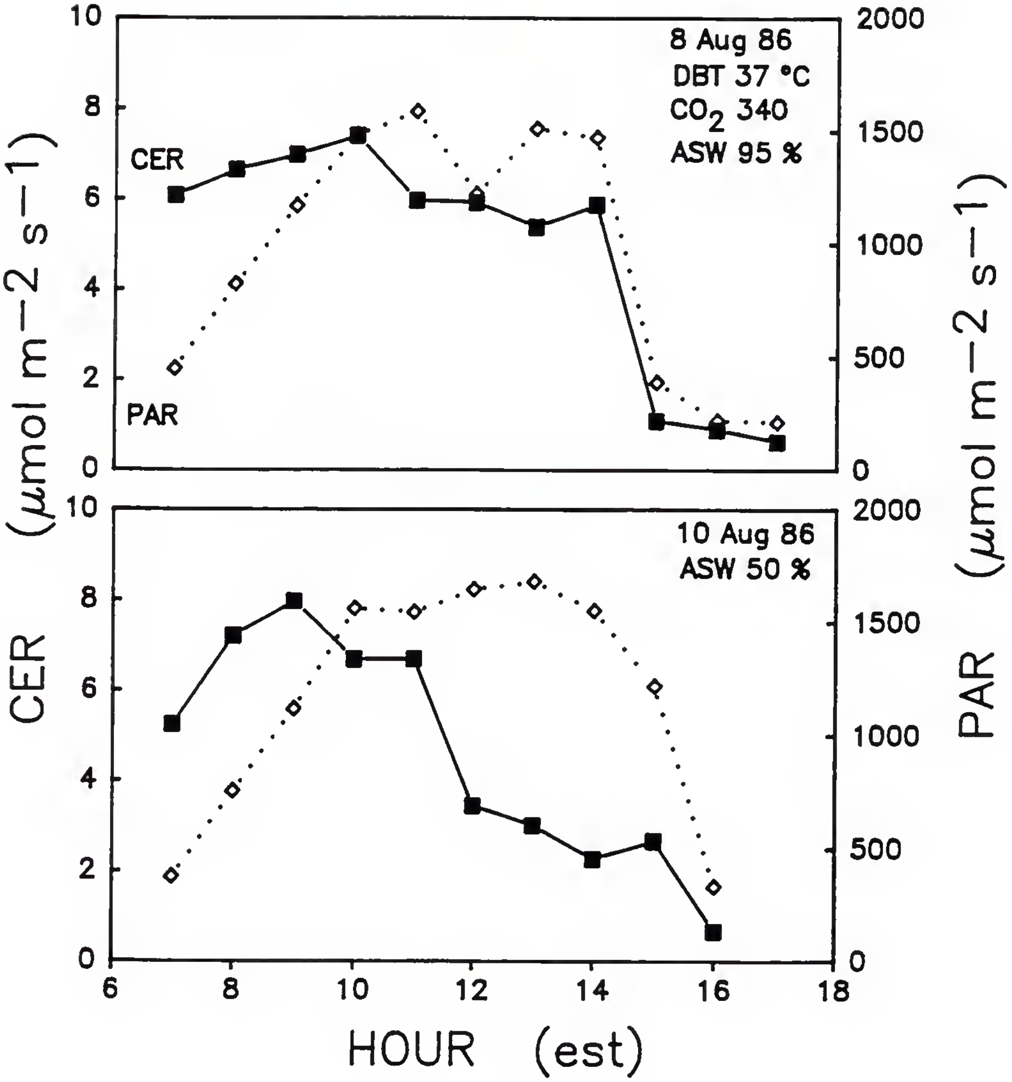


Figure 4.15. Photosynthetic carbon dioxide exchange rates (CER) of fully irrigated (4/4 RVI) citrus trees and photosynthetically active radiation (PAR) at the high dry-bulb temperature (DBT) level and ambient CO_2 concentration on days with high (96%) and low (50%) levels of available soil water (ASW).

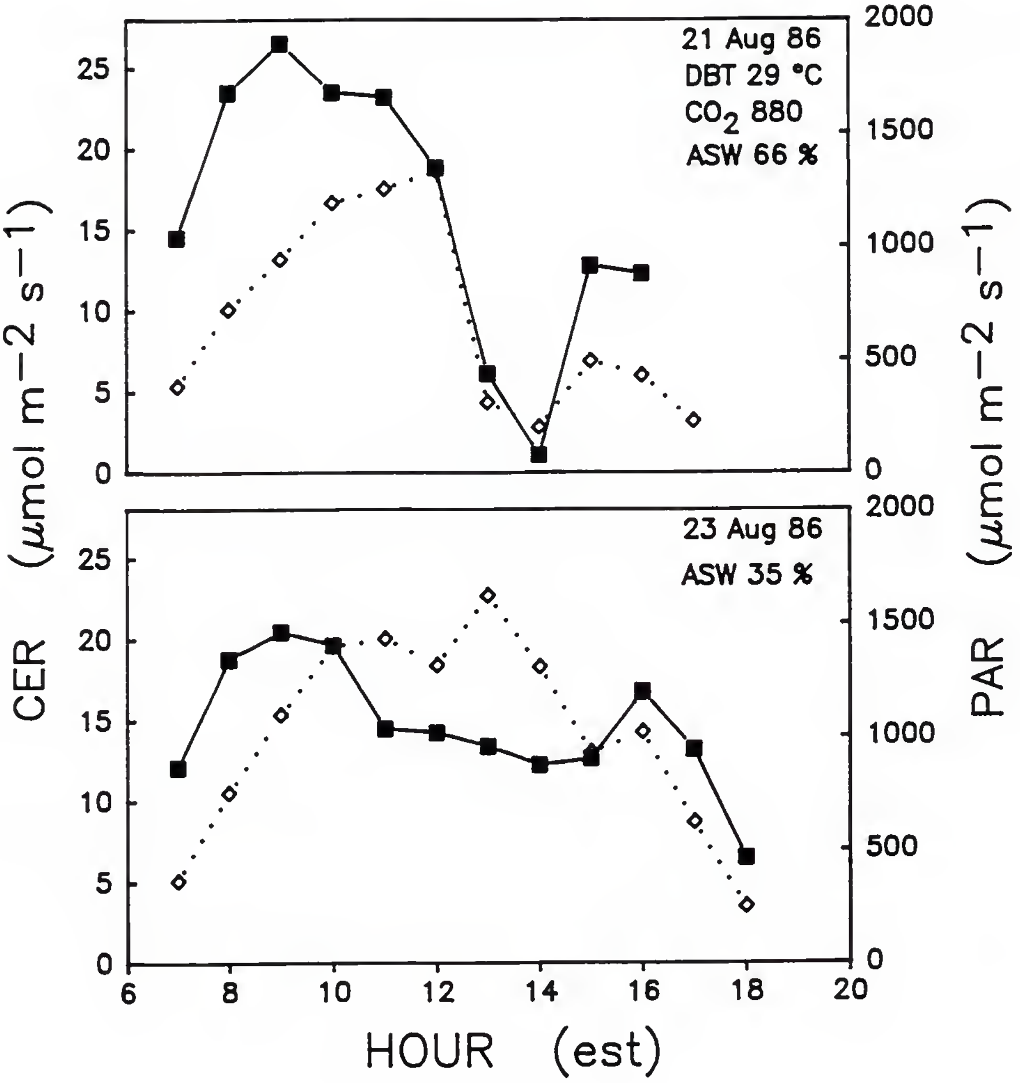


Figure 4.16. Carbon dioxide exchange rates (CER) of fully irrigated (4/4 RVI) citrus trees and photosynthetically active radiation (PAR) at the low dry-bulb (DBT) level and elevated CO_2 concentration on days with high (66%) and low (35%) levels of soil water (ASW).

elevated CO_2 concentration, maximum CERs at high and low soil water contents were reduced compared to rates at low DBT/VPD and elevated CO_2 concentration (Figure 4.17).

Evapotranspiration of citrus trees at both high and low DBT/VPD levels at the ambient CO_2 concentration were only slightly reduced as soil water was depleted (Figure 4.18). Although differences in ET at the low DBT/VPD level and elevated CO_2 concentration as ASW was reduced were confounded by radiation levels (Figure 4.19), it was generally observed that reduction of ET as soil water was depleted at elevated CO_2 concentrations was less severe than at ambient CO_2 (data not shown).

Effects of Partial Irrigation

Gas exchange responses

Because CER and ET are recorded by the system per m^2 of surface area it was necessary to establish that equal leaf area existed in all chambers. Base-line CERs were established by irrigating all compartments of all plants from 14 to 24 June 1986. Daily total ET values for this period are shown in Figure 4.20 and do not reveal any large or consistent differences between chambers. Therefore, nearly equal leaf area in all chambers was assumed. Also, each chamber appeared to have similar leaf area from visual inspection.

Data for 1 August 1986, obtained under the low DBT/VPD and ambient CO_2 conditions, are representative of differences between irrigation treatments at different DBT/VPD levels when all treatments were at nearly equal levels of ASW and are presented in the discussion. Differences in CERs between irrigation treatments were most evident

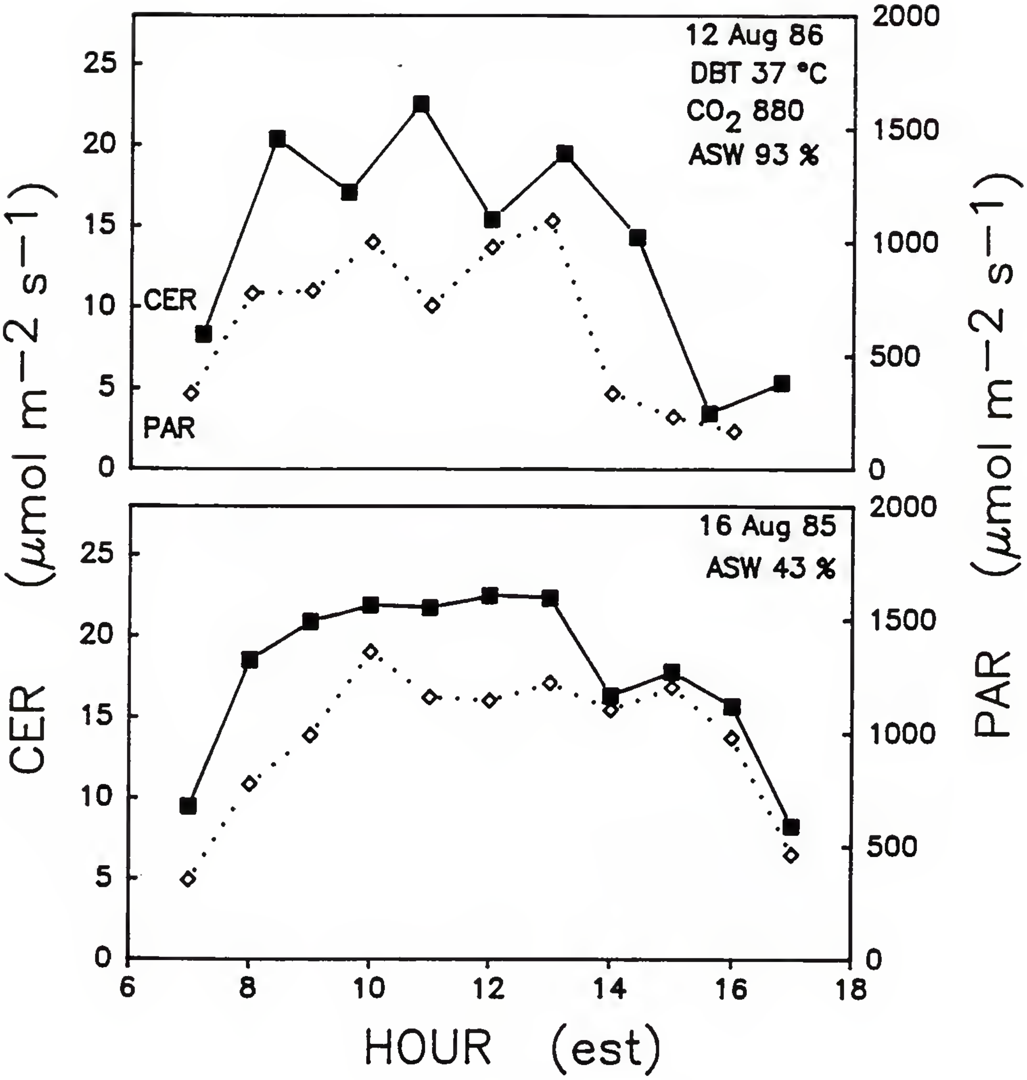


Figure 4.17. Carbon dioxide exchange rates (CER) of fully irrigated (4/4 RVI) citrus trees and photosynthetically active radiation (PAR) at the high dry-bulb temperature (DBT) and elevated CO_2 concentration on days with high (93%) low (43%) levels of avialable soil water (ASW).

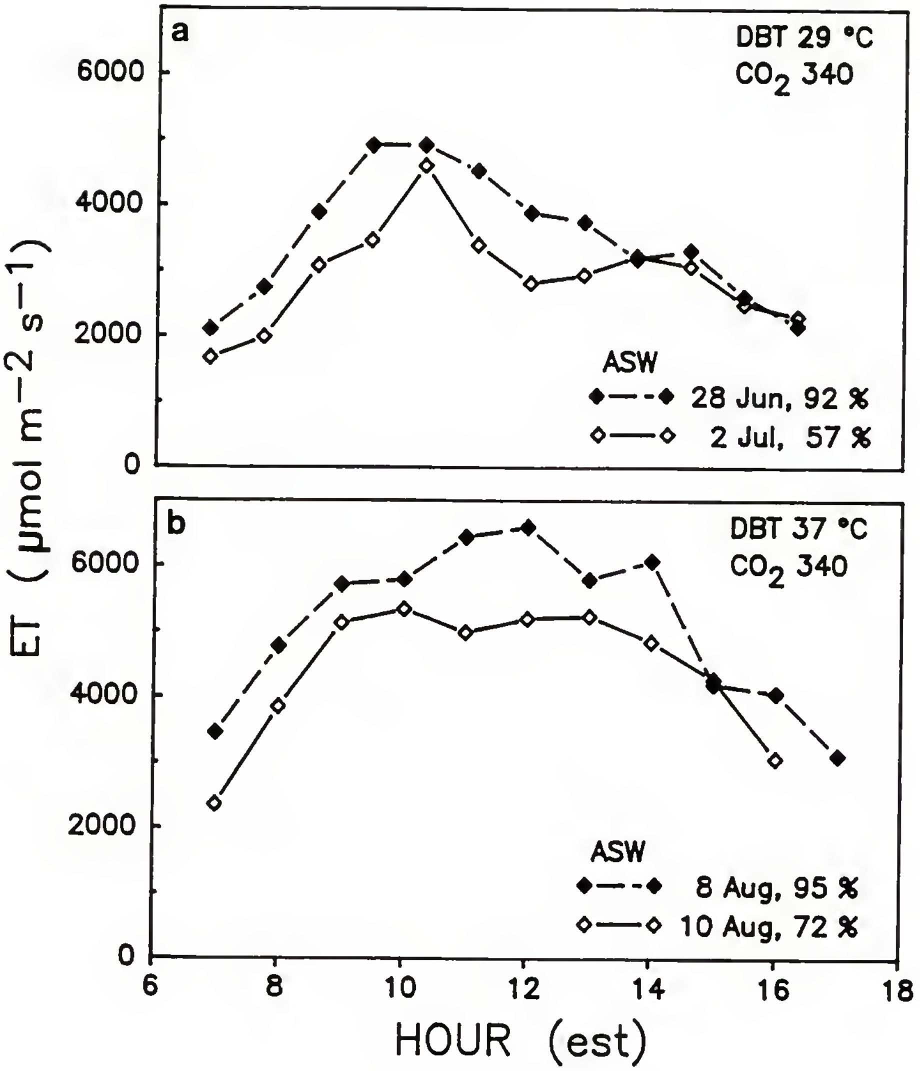


Figure 4.18. Evapotranspiration (ET) of fully irrigated (4/4 RVI) citrus trees at high and low levels of available soil water (ASW) and:
a) low dry-bulb temperature (DBT) and ambient (340 μmol mol^{-1}) CO_2 concentration,
b) high dry-bulb temperature (DBT) and ambient CO_2 concentration.

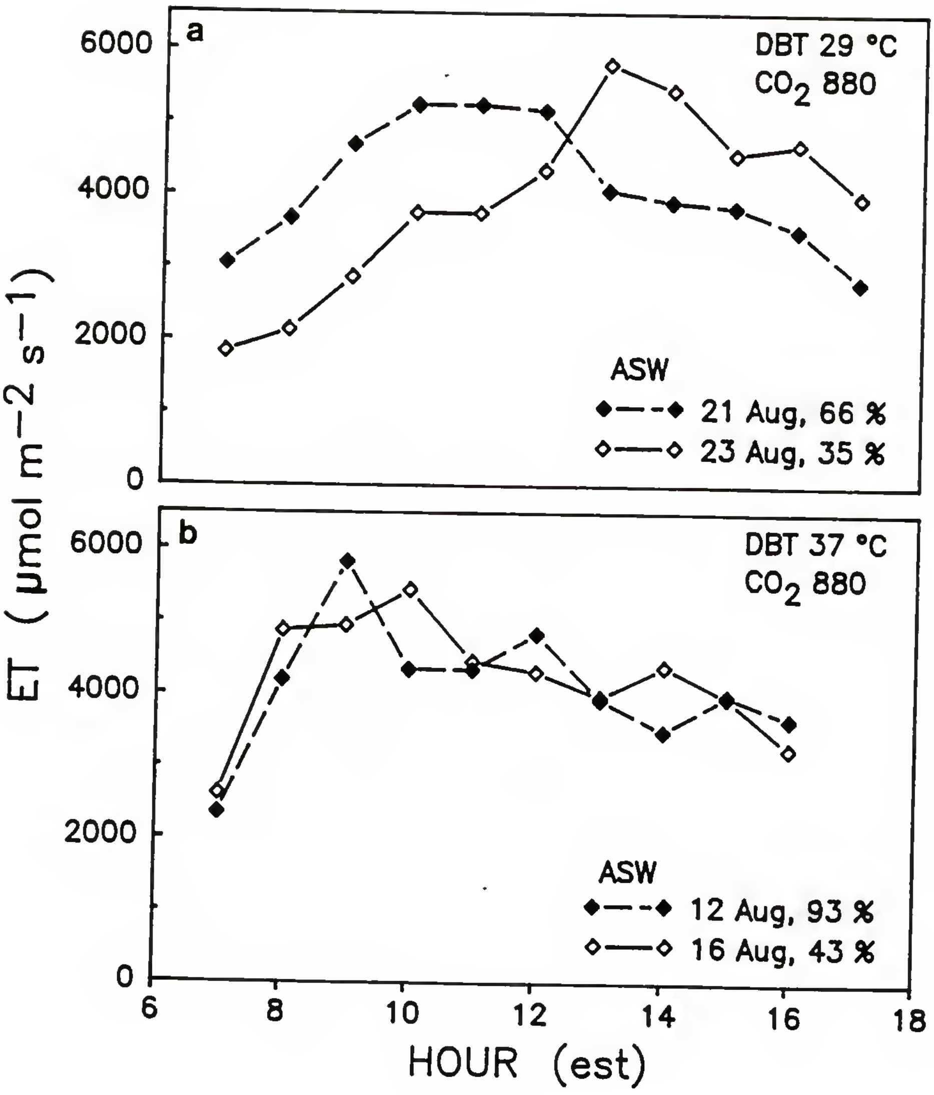


Figure 4.19. Evapotranspiration (ET) of fully irrigated (4/4 RVI) citrus trees at high and low levels of available soil water (ASW) and:

a) low dry-bulb temperature (DBT) and elevated (880 mol mol^{-1}) CO_2 concentration,

b) high DBT and elevated CO_2 concentration.

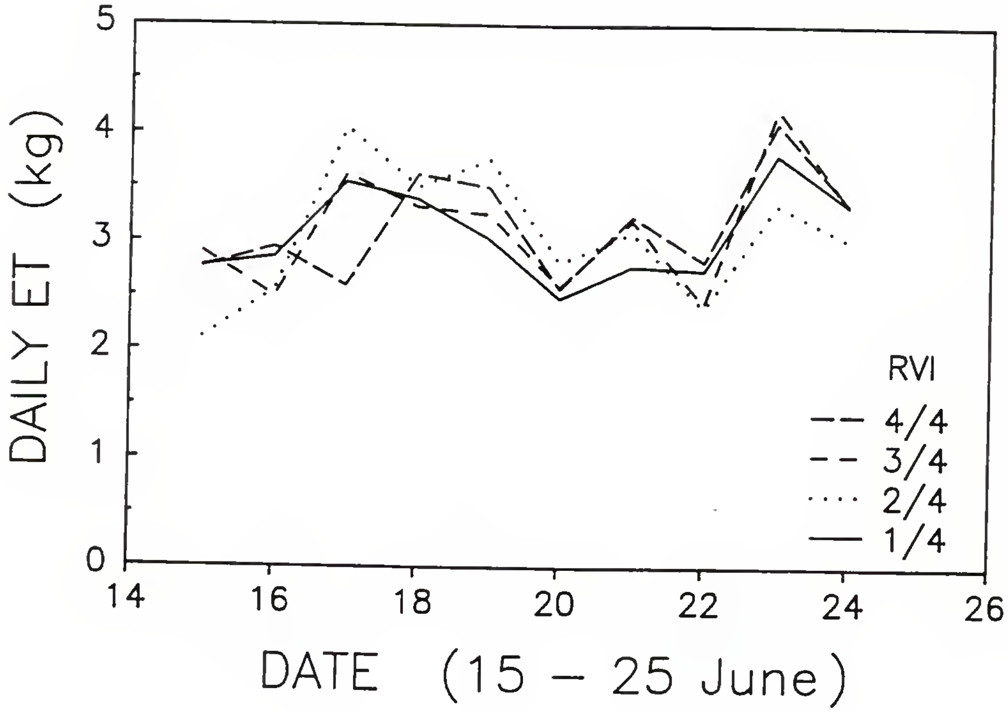


Figure 4.20. Daily total evapotranspiration (ET) of citrus trees in separate chambers prior to initiation of partial rooting-volume-irrigation (RVI) treatments.

during the morning hours and least evident after 1200 EST due to severe midday depression of CERs. Throughout the study, maximum mid-morning CERs were consistently highest for the 4/4 RVI treatment and lowest for the 1/4 RVI treatment. In general, even when ASW was nearly two-thirds depleted in the 4/4 RVI treatment, CERs did not drop to levels as low as those that occurred at comparably low levels of ASW in the 1/4 RVI treatment. Even immediately after irrigating, CERs in the partially irrigated treatments were not as great as those that occurred in the 4/4 RVI treatment (Figure 4.21).

Differences between the partially irrigated treatments were less distinct. During the middle of the day, when CERs were typically reduced in all treatments, differences were minimal or inconsistent between the 3/4 and 2/4 and 1/4 RVI treatments. Typically, CERs were very similar in the 2/4 and 3/4 RVI treatments throughout most of the season. This is attributed to the variability in the volume of roots actually occupying each of the four compartments (22 to 33% of the total root mass) as indicated by plants harvested before initiation of the treatments. In general, when soil water was more than 30% depleted in the 1/4 RVI treatment, CERs dropped below those of all other treatments, but immediately after irrigating they approached CERs obtained by the 2/4 and 3/4 irrigated plants. Dry-bulb temperatures in all chambers rose sharply between 1000 and 1100 EST which resulted in a marked increase in VPD in all chambers. Dry-bulb temperatures in chambers with 2/4 and 1/4 RVI treatments rose 1 to 3 °C above temperatures in chambers with the other treatments and resulted in VPDs which were at times nearly 1.0 kPa

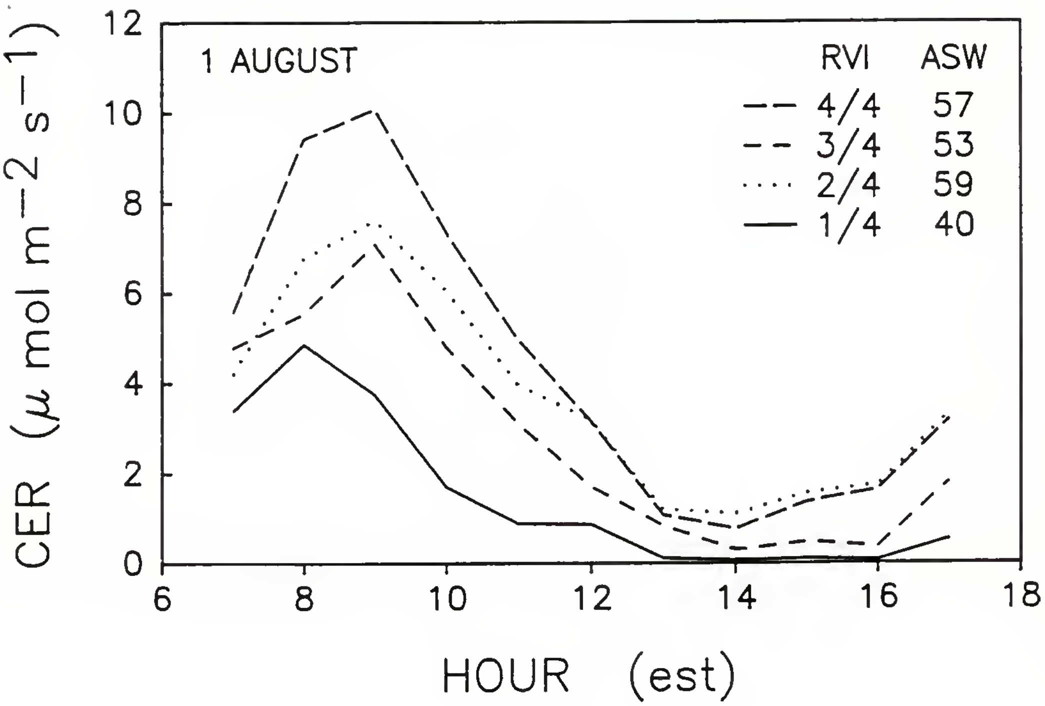


Figure 4.21. Carbon dioxide exchange rates (CER) of citrus trees at various levels of rooting-volume-irrigation (RVI) at nearly equal levels of available soil water (ASW) on 1 August 1986 at the low dry-bulb temperature and ambient CO_2 concentration.

greater than in the other treatments and may have contributed significantly to differences in CERs between the fully and least irrigated treatments (Figure 4.22).

The performance of the partially irrigated trees in the present study may have been improved by maintaining higher levels of soil water content. This is true in particular for trees with only one-quarter of their root system irrigated. These plants experienced soil water stress more frequently and more severely than the other treatments. Because of the low water holding capacity of the soil it was possible for this treatment to lose as much as a third of the ASW during one day and fall below the critical soil water level before being irrigated. Keeping this treatment at higher soil water levels may have improved its performance.

Evapotranspiration rates were generally greatest for the 4/4 RVI treatment and lowest for the 1/4 RVI treatment, but varied inconsistently and only slightly between the 2/4 and 3/4 treatments (Figure 4.23). Both morning and afternoon stomatal conductances were very low in all treatments. Morning values (measured between 0800 and 1200 EST) ranged from 0.016 to 0.177 cm s^{-1} and afternoon values (measured between 1200 and 1500 EST) ranged from 0.009 to 0.078 cm s^{-1} (Table 4.1). Although stomatal conductance in citrus is typically low, the values obtained during this study are extremely low and indicate that plants were severely stressed. Total water used for each treatment during the entire 94-day period of study ranged from 544 kg for the fully watered plants to 504 kg for plants with 1/4 RVI (Table 4.2). Irrigation frequency increased with reduction in root volume irrigated and was twice as great for the 1/4 RVI treatment as for the fully

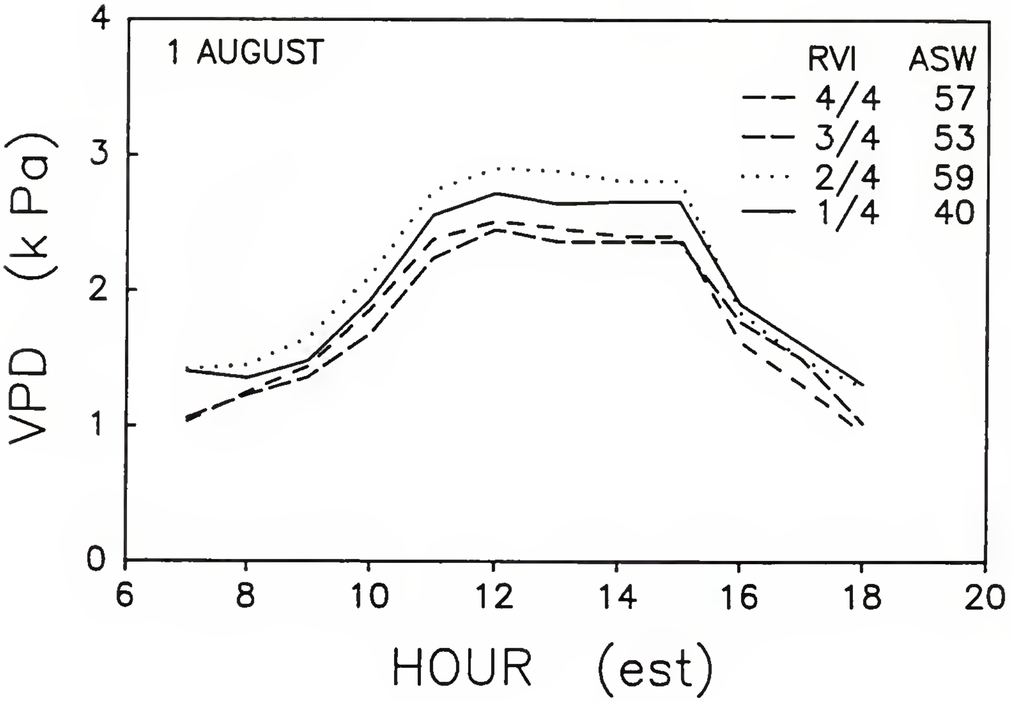


Figure 4.22. Atmospheric water vapor pressure deficit (VPD) conditions in growth chambers with citrus trees at various levels of rooting-volume-irrigation (RVI) and nearly equal levels of available soil water (ASW) on 1 August 1986 at the low dry-bulb temperature and ambient CO_2 concentrations.

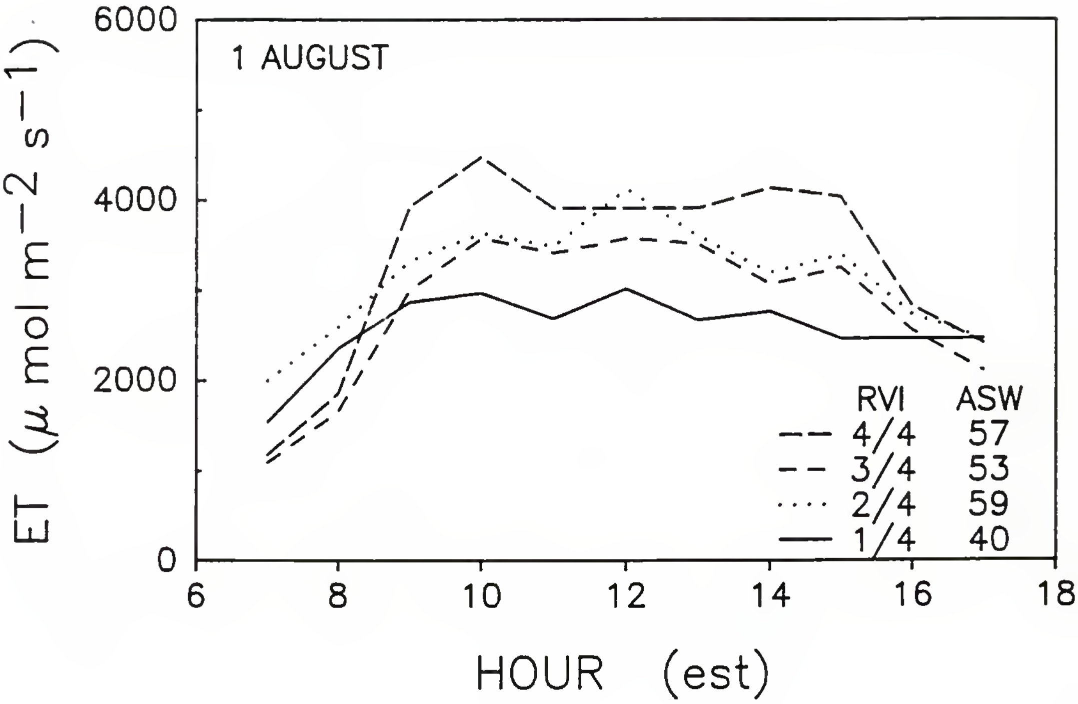


Figure 4.23. Evapotranspiration rates (ET) of citrus trees various levels of rooting-volume-irrigation (RVI) and nearly equal levels of available soil water (ASW) on 1 August 1986 at the low dry-bulb temperature and ambient CO_2 concentration.

Table 4.1. Stomatal conductance of citrus trees with various fractions of their rooting volume irrigated (RVI).

		$cm\ s^{-1}$				
Date	Time	4/4 RVI	3/4 RVI	2/4 RVI	1/4 RVI	1/4+ RVI
07 Jul 86	1300-1500	0.52	0.51	0.052	0.052	0.077
15 Jul 86	0800-1000	0.177	0.109	0.117	0.131	-----
21 Jul 86	1300-1500	0.009	0.021	0.014	0.011	-----
23 Jul 86	1300-1400	0.022	0.012	0.016	0.033	0.025
25 JUl 86	1000-1200	0.011	0.011	0.012	0.013	0.014
29 Jul 86	0900-1100	0.064	0.092	0.033	0.028	-----
30 Jul 86	1300-1435	0.025	0.014	0.035	0.010	0.017
31 Jul 86	0900-1100	0.060	0.060	0.061	0.079	0.016
06 Aug 86	1230-1430	0.042	0.038	0.052	0.019	0.041
11 Aug 86	1100-1300	0.020	0.043	0.078	0.023	0.024
18 Aug 86	1035-1200	0.055	0.037	0.037	0.042	0.035

Table 4.2 Cumulative and daily evapotranspiration (ET), irrigation frequency, and seasonal water-use efficiency (WUE) of citrus trees with various fractions of their rooting volume irrigated (RVI) from June 14 to September 15 1986.

RVI	Total ET kg	Total ET mm	Mean ET mm/day	Irrigations #	Biomass g	WUE g kg^{-1}
4/4	544.4	272.2	2.9	20	945	1.74
3/4	483.3	241.6	2.6	23	775	1.60
2/4	513.6	256.7	2.7	30	558	1.09
1/4	504.2	252.1	2.7	40	505	1.00
1/4+	620.0	310.0	3.3	27	449	0.72

Seasonal WUE = New shoot biomass (g)/Total ET (kg) irrigated treatment. Water-use efficiency varied between treatments during the early morning hours and was greatest for the fully irrigated plants and least for the 1/4 RVI treatment. After 1100 to 1200 EST differences in WUE between treatments were minimal (Figure 4.24). Seasonal WUE on a mass basis [g (new shoot biomass) kg^{-1} (ET)] was greatest for fully irrigated plants and was reduced with reduction of the irrigated rooting volume (Table 4.2).

The effect of soil water depletion on CERs in each of the irrigation treatments is summarized by plots of diurnal CERs at high and low levels of ASW for each irrigation level. Maximum photosynthesis in all treatments under these atmospheric conditions, at all levels of soil water content, occurred before 1200 EST. It is readily apparent that depletion of ASW had the greatest effect in each treatment on morning CERs and that closure of stomata during midday became more severe as water stress increased (Figures 4.25 through 4.28).

Partial irrigation with and without a grass cover

Figure 4.29 shows atmospheric conditions in the chambers occupied by the 1/4 RVI and 1/4 RVI plus grass cover treatments. Dry-bulb temperature and VPD were slightly higher in the treatment without grass cover during the early part of the study and reflect the higher water use by the 1/4 RVI+ treatment. The St. Augustine grass cover in the 1/4+ RVI treatment occupied a surface area of approximately 1.5 m^2 and contributed significantly to the CERs obtained in this treatment. The combined maximum midmorning CERs of the 1/4 RVI citrus trees with St. Augustine grass cover were often three times higher than those obtained

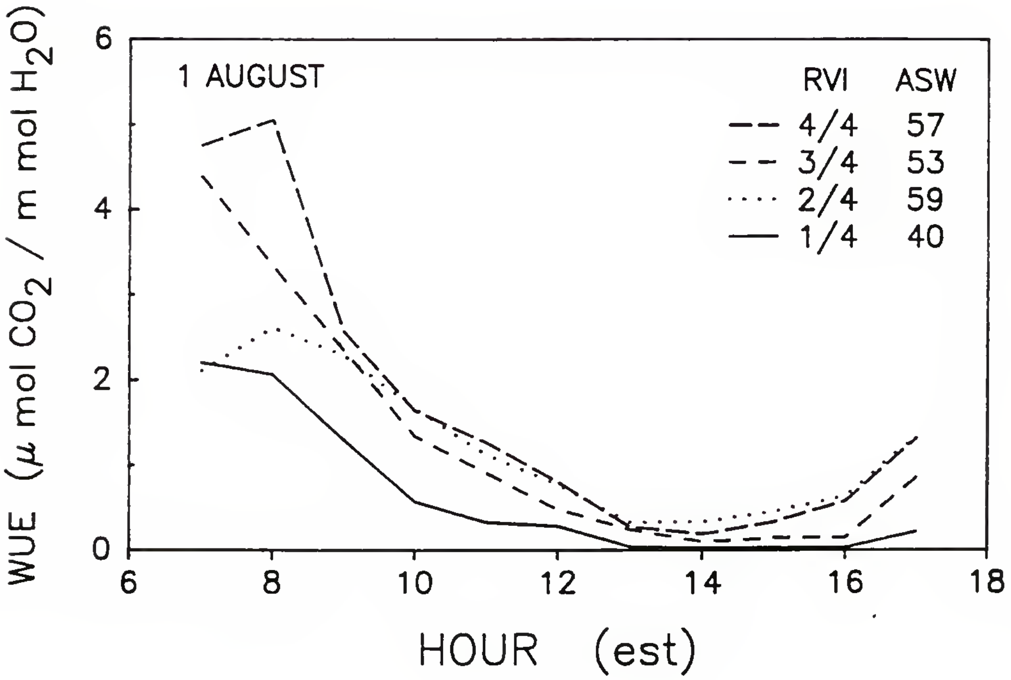


Figure 4.24. Water-use efficiency (WUE) of citrus trees at various levels of rooting-volume-irrigation (RVI) and nearly equal levels of available soil water (ASW) on 1 August 1986 at the low dry-bulb temperature and ambient CO_2 concentration.

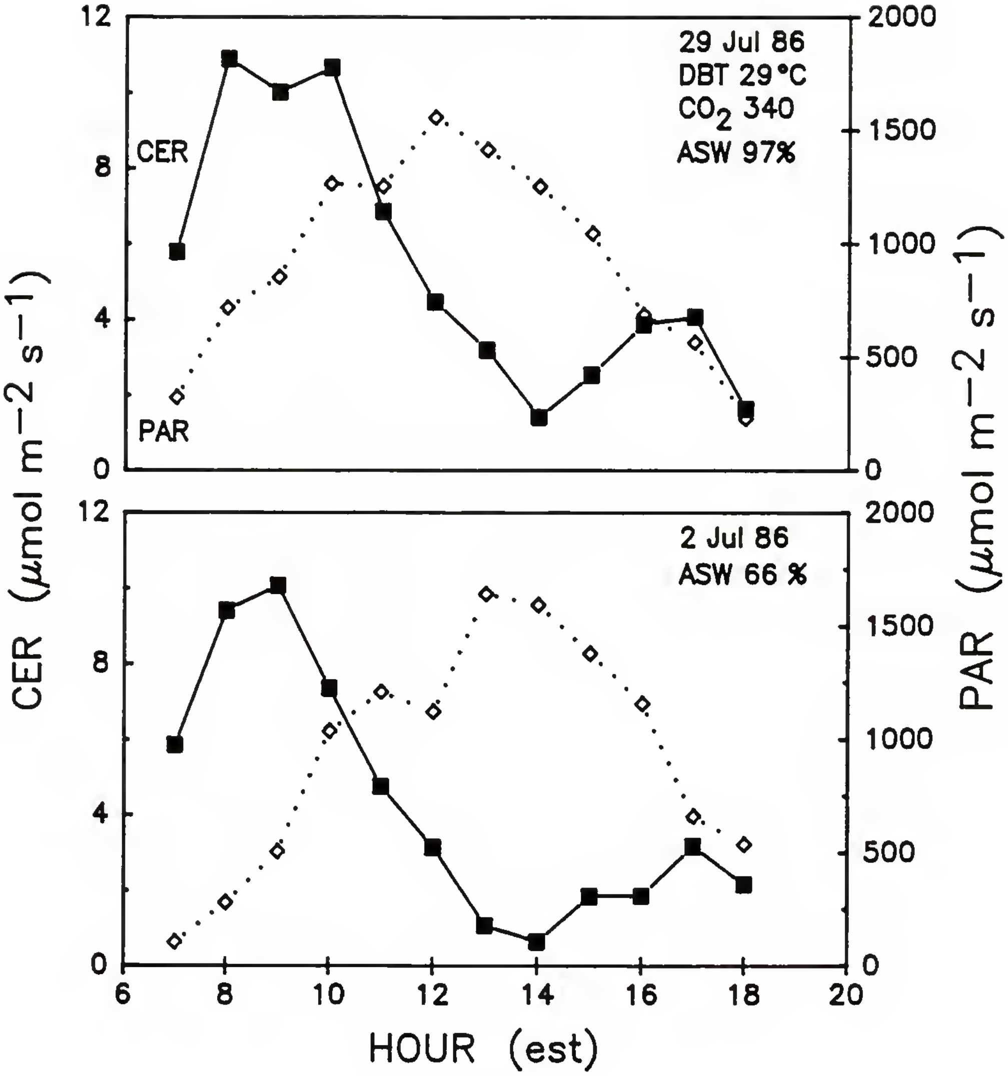


Figure 4.25. Carbon dioxide exchange rates (CER) of citrus trees and photosynthetically active radiation (PAR) in the 4/4 rooting-volume-irrigated treatment at the low dry-bulb temperature (DBT) and ambient CO_2 concentration at high (97%) and low (66%) levels of available soil water (ASW).

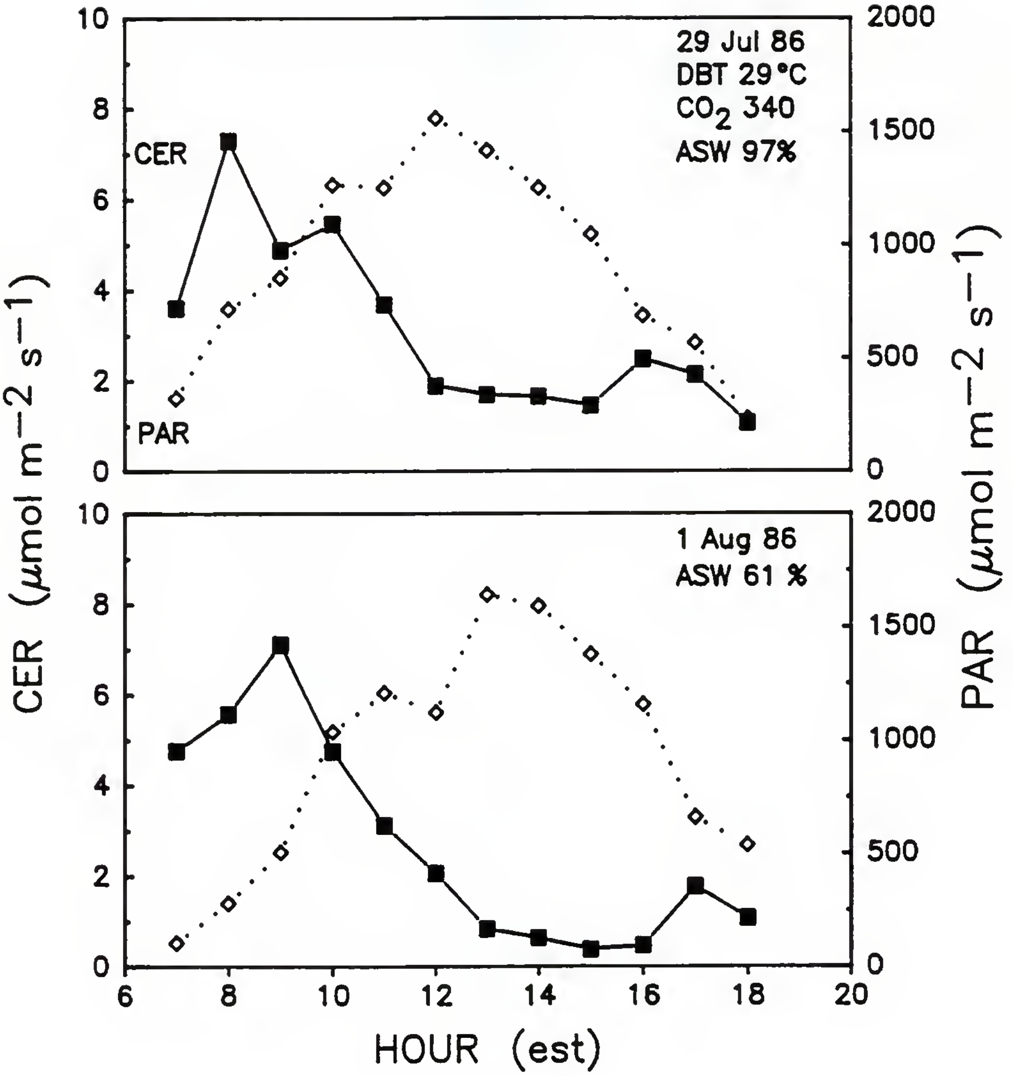


Figure 4.26. Carbon dioxide exchange rates (CER) of citrus in the 3/4 rooting-volume-irrigated treatment at the low dry-bulb temperature (DBT) and ambient CO_2 concentration on days with high (97%) and low (61%) levels of available soil water.

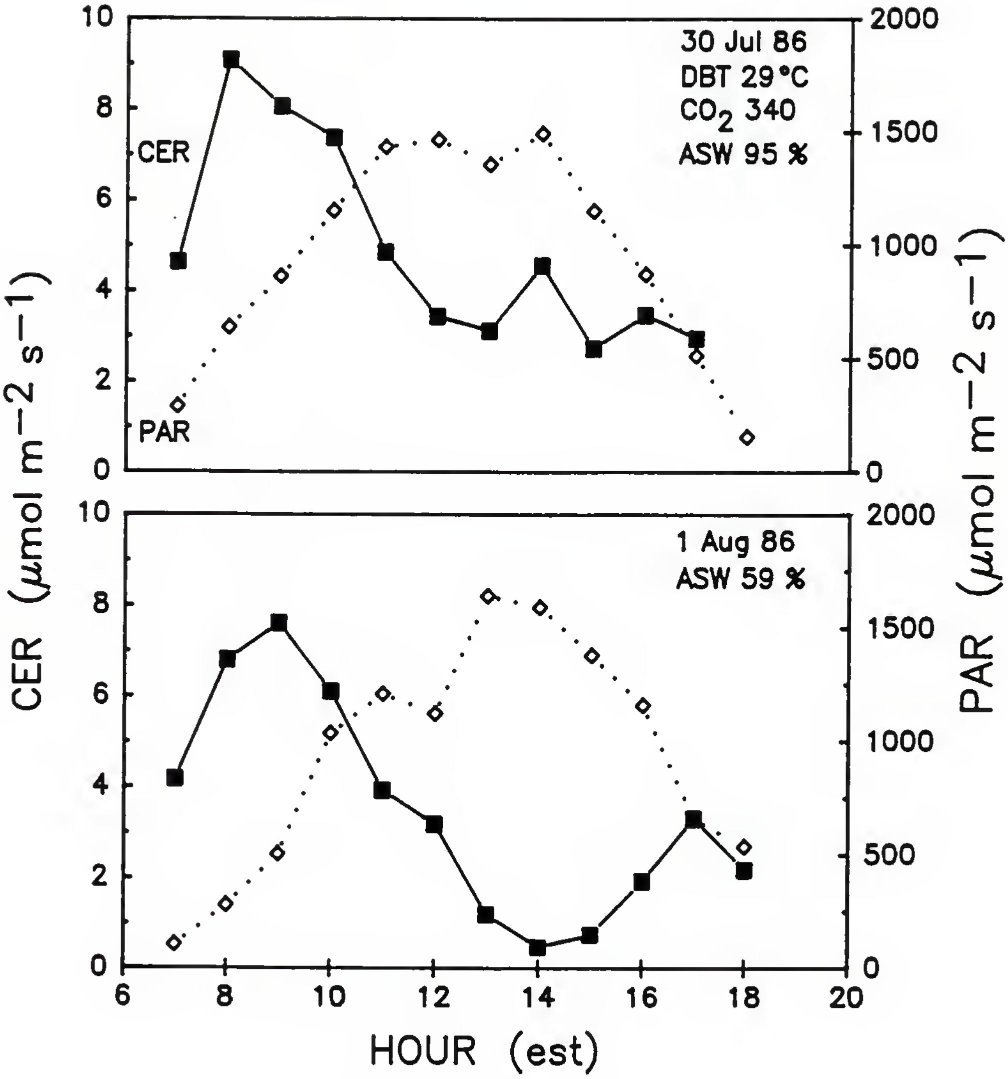


Figure 4.27. Carbon dioxide exchange rates (CER) of citrus trees in the 2/4 rooting-volume-irrigated treatment at the low dry-bulb temperature (DBT) and ambient CO_2 concentration on days with high (95%) and low (59%) levels of available soil water ASW.

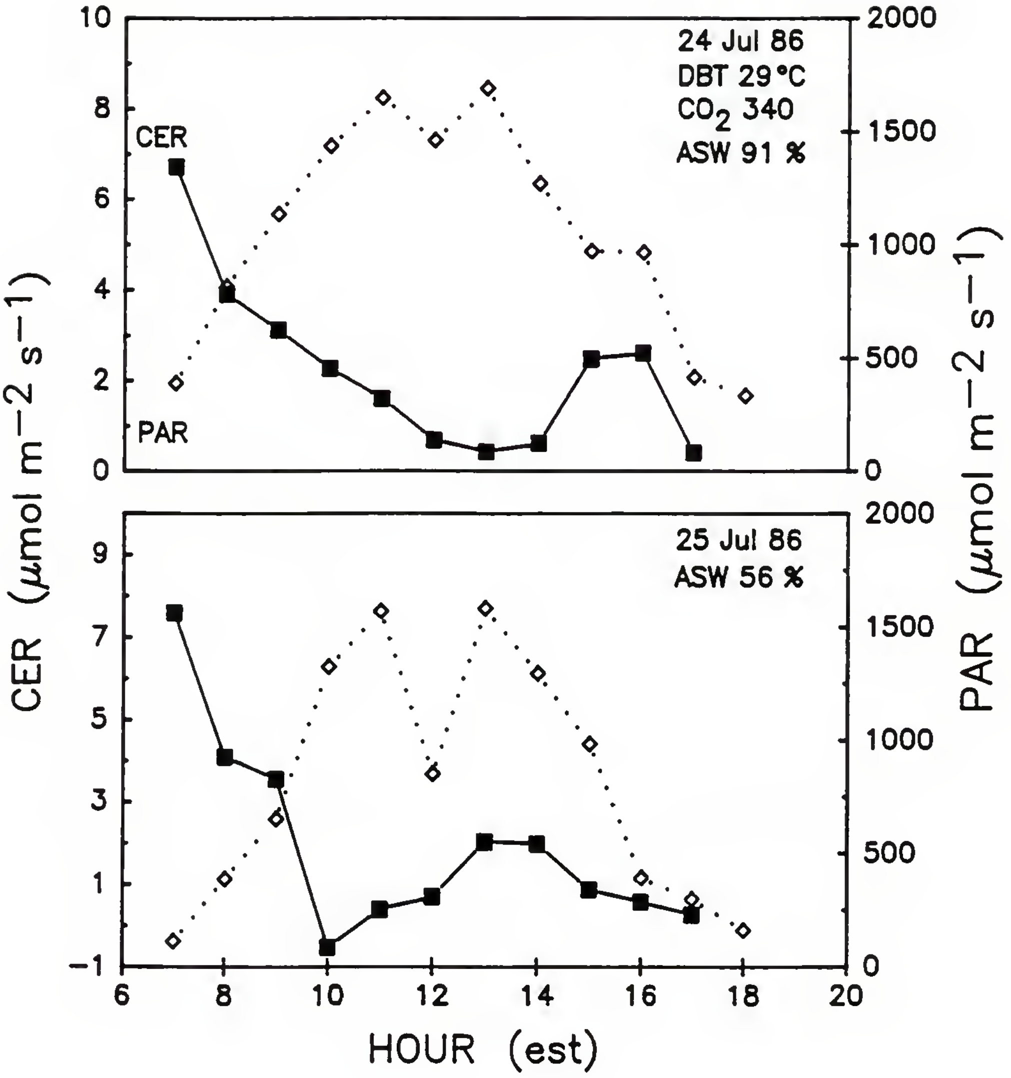


Figure 4.28. Carbon dioxide exchange rates (CER) of citrus trees in the 1/4 rooting-volume-irrigated treatment at the low dry-bulb temperature (DBT) and ambient CO_2 concentration on days with high (91%) and low (56%) levels of available soil water (ASW).

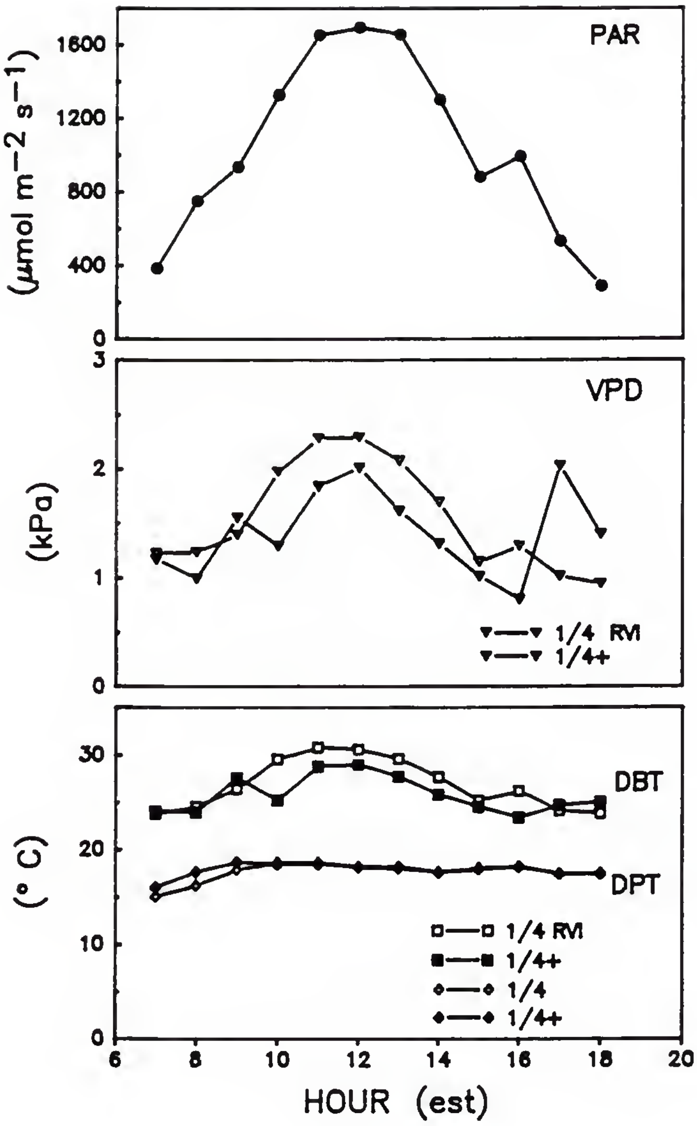


Figure 4.29. Environmental conditions in chambers occupied by the 1/4 and 1/4+ rooting-volume-irrigated treatments on 28 June 1989:
a) Photosynthetically active radiation (PAR),
b) Atmospheric water vapor pressure deficit (VPD),
c) Dry-bulb and dewpoint temperature (DBT and DPT, respectively).

from the 1/4 RVI treatment without grass cover early in the season (Figure 4.30). Evapotranspiration rates in the 1/4 RVI with grass cover typically rose throughout the morning and into the afternoon whereas ET in the 1/4 RVI without grass remained constant throughout the diurnal period of greatest evaporative demand. Evapotranspiration in the 1/4+ RVI was frequently twice as great as in the 1/4 RVI without grass until late in the study when the grass cover began dying in the nonirrigated compartments (Figure 4.30). Water-use efficiency of the citrus plus St. Augustine grass system was considerably higher throughout the day (Figure 4.30). Total water use for the 1/4 RVI with grass cover was greater than for any partially irrigated treatment and 75 kg greater than the fully irrigated treatment. When plants were sampled at the end of the study the irrigated compartment of the 1/4 RVI with grass treatment contained a dense mat of St. Augustine grass roots. This mass of roots may have contributed to water retention in the very porous soil but also represented competition with citrus roots for the available soil water. Although seasonal water use was over 100 kg greater in the 1/4 RVI with grass than in the same treatment without grass, both mean new citrus leaf area per plant and total new citrus tissue dry matter were lower in the 1/4 + RVI treatment than in the 1/4 RVI without grass treatment. Consequently, total seasonal water use efficiency on a mass basis [g (new shoot biomass) kg^{-1} (ET)] was 1.0 for the 1/4 treatment without grass cover and 0.72 for the 1/4 RVI treatment with grass cover (Table 4.2). This suggests that considerable competition for soil water

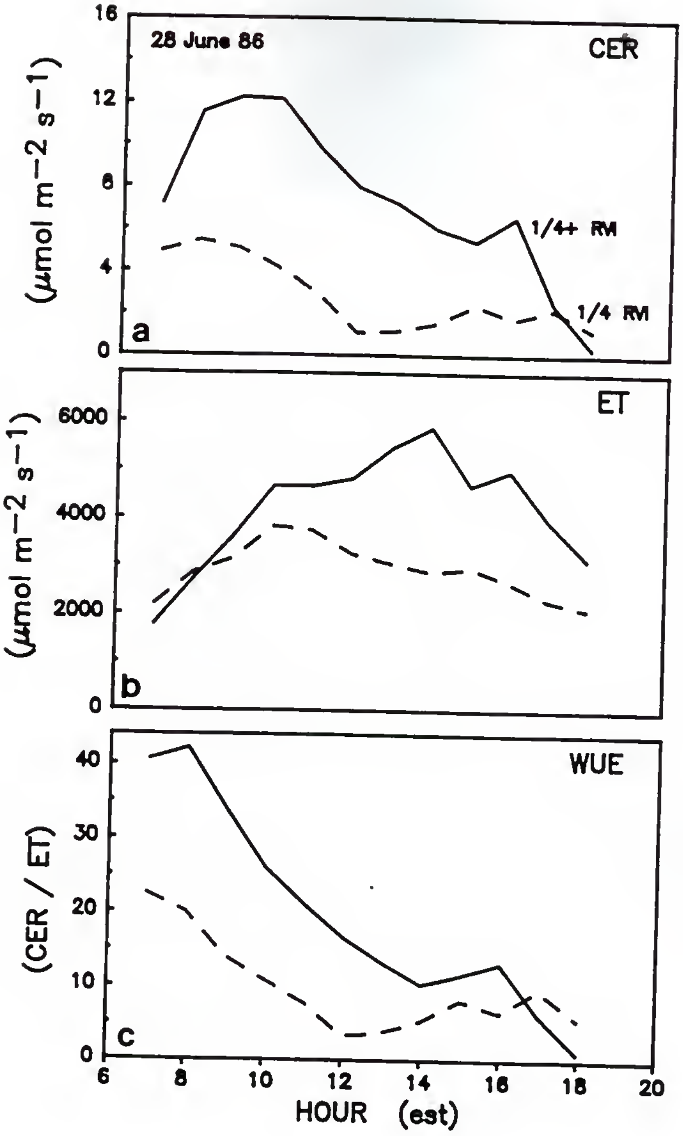


Figure 4.30. Gas exchange responses of citrus trees in the 1/4 and 1/4+ rooting-volume-irrigated treatment on 28 June 1986:
a) Photosynthetic carbon exchange rate (CER),
b) Evapotranspiration (ET),
c) Water-use efficiency (WUE, µmol CO_2/mmol H_2O).

between roots of a grass cover crop and young citrus trees may exist on sandy soils when the cover crop is grown on the areas were citrus roots are concentrated.

Biomass Accumulation

Leaf area index in each chamber, calculated from plants sampled at the end of the study, are reported in Table 4.3. When plants were harvested at the end of the study, two of the plants from the 1/4 RVI treatment and one from the 2/4 RVI treatment were found to have leaky compartments, indicating that plants in these containers actually received more water than the rest of the trees in their treatment. When these trees were removed from calculations LAIs were slightly reduced as indicated by the corrected LAI values. Trees in the 2/4 RVI treatment experienced higher temperatures and water stress during the last 2 weeks of the study than in other treatments which resulted in severe leaf drop.

Simple linear regression was used to analyze the relationship of new leaf area and new biomass accumulation per plant to the percentage rooting volume irrigated. Plants which had leaky compartments were eliminated from these determinations. A significant linear relationship existed between the leaf area and dry weight of new leaves per plant, the dry weight of new stems per plant, the total new shoot mass per plant and the percent rooting volume irrigated (Table 4.3).

Statistical differences in biomass accumulation between rootstock cultivars were found only in the 1/4 and 1/4+ RVI treatments. Within the 1/4 RVI treatment, area and dry weights of new leaves and dry weight of

Table 4.3 Citrus biomass data: mean dry wt. per plant and r^2 of linear regressions of leaf area or biomass data vs. percentage rooting volume irrigated (RVI)

	4/4 RVI	3/4 RVI	2/4 RVI	1/4 RVI	1/4+ RVI	r^2
LAI m^2 m^{-2}	7.70	5.82	4.57	3.04	4.68	
LAI (corrected)	7.70	5.82	4.32	2.72	4.68	
	m^2 plant^{-1}					
New Leaf Area	0.426	0.334	0.196	0.222	0.187	0.8679*
Std. dev.	(0.186)	(0.105)	(0.094)	(0.093)	(0.064)	
	g plant^{-1}					
New Lvs.	32.93	26.41	17.42	17.52	14.01	0.9237**
Std. dev.	(15.69)	(11.68)	(8.92)	(7.71)	(4.24)	
New Stems	11.56	9.06	8.31	6.36	7.37	0.9291**
Std. dev.	(6.46)	(3.90)	(4.87)	(3.04)	(3.12)	
Stems + Lvs.	45.00	36.92	26.56	24.03	21.38	0.9666**
Std. dev.	(22.84)	(15.49)	(14.26)	(10.32)	(6.47)	

* Significant at $p = 0.05$

** Significant at $p = 0.01$

† Means of the 1/4+ RVI treatment are shown here but were not included in regression analyses.

new stems were greater for plants on either Carrizo citrange or Swingle citrumelo than for those on sour orange (Figures 4.31 through 4.34). Within the 1/4+ RVI treatment, area and dry weights of new leaves and dry weight of new stems were greater for plants on Swingle citrumelo than those on either Carrizo citrange or sour orange. It appears that biomass accumulation of plants in the 1/4 and 1/4+ RVI treatments was reduced less for plants on Swingle than for those on sour orange. In all treatments except the 2/4 RVI treatment, new tissue production of plants on sour orange rootstock was less than that of plants on Carrizo citrange or Swingle citrumelo. In the 2/4 RVI heavy leaf drop during the last two weeks of the study probably reduced rootstock differences. The results suggest that plants on Swingle citrumelo rootstocks performed better under partial rooting volume irrigation than plants on sour orange. Root dry weight (old + new roots) was generally greatest for Swingle citrumelo followed by Carrizo citrange and then sour orange (Figure 4.35). Because these data represent root growth both before and after initiation of partial rooting volume treatments it is not certain whether roots of Swingle citrumelo grew better than those of either Carrizo citrange or sour orange after initiation of irrigation treatments. If plants on Swingle citrumelo began the study with greater root mass than plants on the other two rootstocks this may explain differences observed in leaf and stem growth after treatment initiation.

Root Hydraulic Conductivity

Mean root hydraulic conductivities were calculated on a root length basis and are reported in Table 4.4 as mg root exudate m^{-1} root

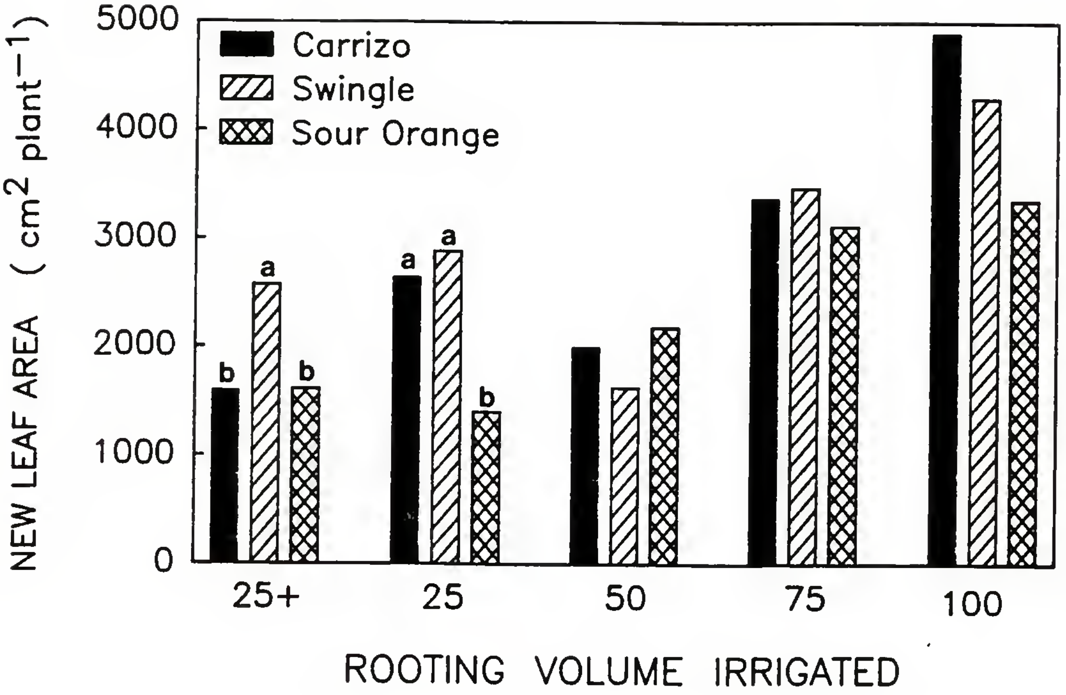


Figure 4.31. Total new leaf area accumulated by citrus trees on three different rootstock cultivars with various fractions of their rooting volume irrigated.

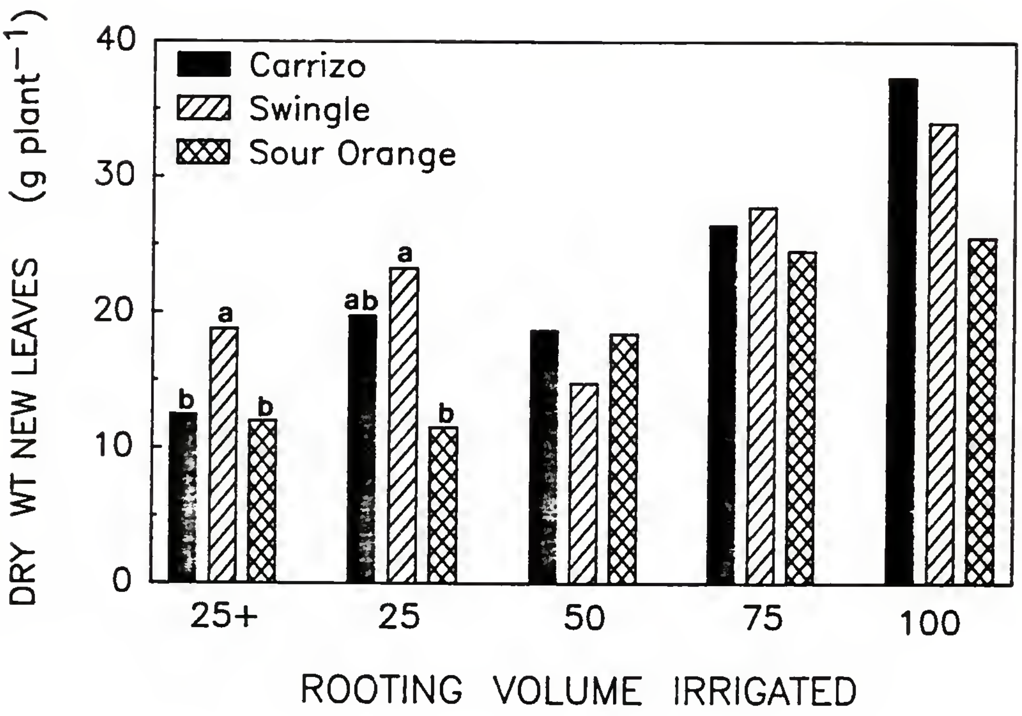


Figure 4.32. Total new leaf dry weight of citrus trees on three different rootstock cultivars with various fractions of their rooting volume irrigated.

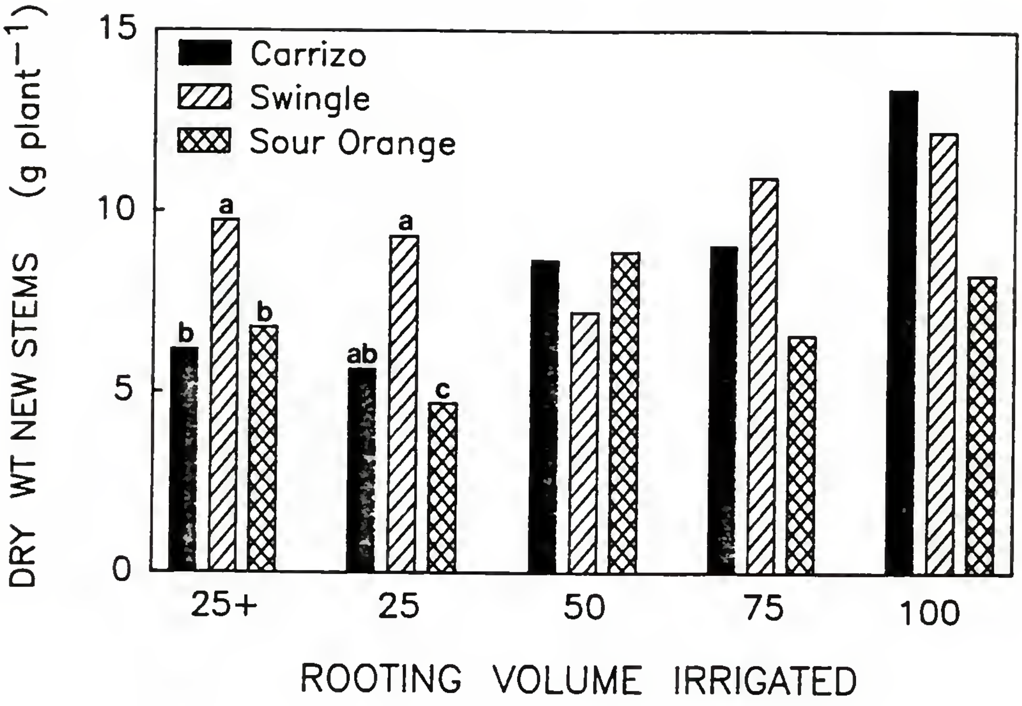


Figure 4.33. Total new stem dry weight of citrus trees on three different rootstock cultivars with various fractions of their rooting volume irrigated.

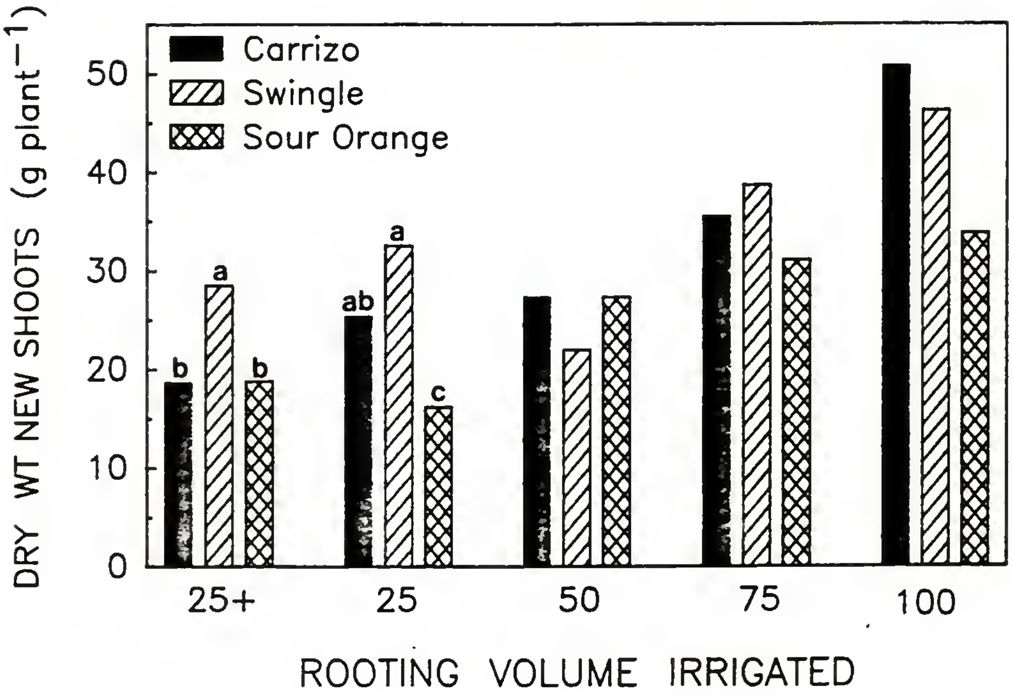


Figure 4.34. Total new shoot (leaves + stems) dry weight of citrus trees on three different rootstock cultivars with various fractions of their rooting volume irrigated.

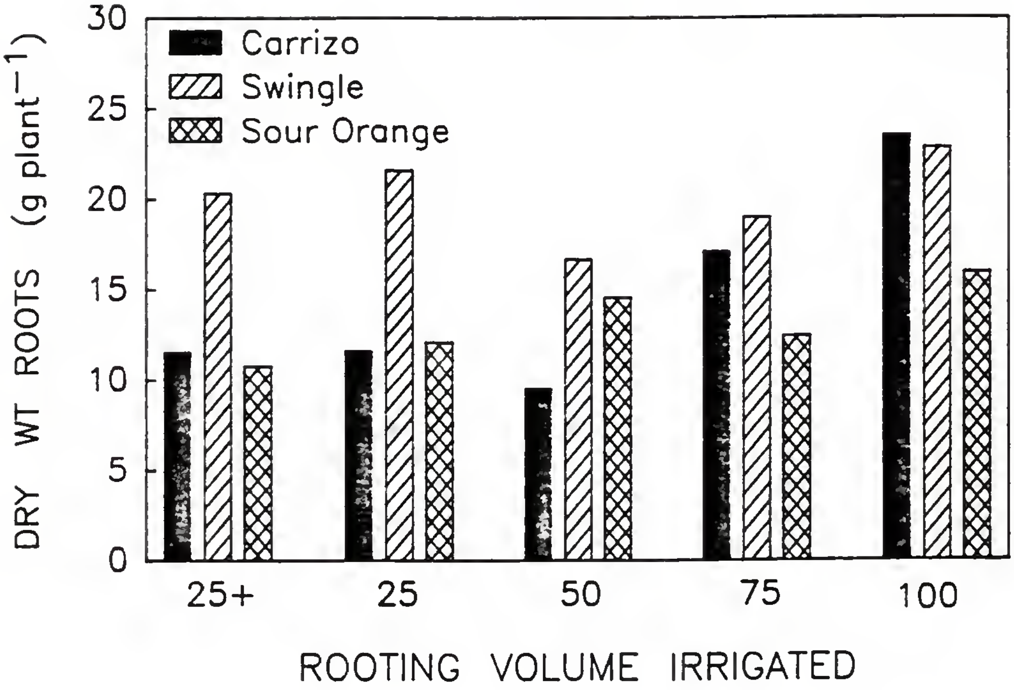


Figure 4.35. Total (new + old) root dry weight of citrus trees on three different rootstock cultivars with various fractions of their rooting volume irrigated.

Table 4.4 Mean root hydraulic conductivity [mg (root exudate) m^{-1} (root length) s^{-1} MPa^{-1} (pressure applied)] of irrigated and nonirrigated roots of citrus trees with various fractions of their rooting volume irrigated (RVI).

	4/4 RVI	3/4 RVI	2/4 RVI	1/4 RVI	1/4+ RVI
	mg m^{-1} s^{-1} MPa^{-1}				
			Irrigated Roots		
Mean	245.7	184.3	299.9	223.1	145.9
Std. dev.	(155.5)	(84.2)	(189.2)	(132.9)	(97.2)
			Nonirrigated Roots		
Mean	----	55.4	141.0	124.5	107.4
Std. dev.	----	(31.7)	(109.6)	(78.7)	(76.0)

length s^{-1} MPa^{-1}. Simple linear regression analysis of the relation between hydraulic conductivity of roots to the fraction of total rooting volume irrigated was performed separately for irrigated and nonirrigated roots but revealed no significant linear trend in either case. Mean conductivities of the irrigated roots ranged from 145.9 to 299.9 mg m^{-1} s^{-1} MPa^{-1} and for nonirrigated roots values ranged from 55.4 to 141.0 mg m^{-1} s^{-1} MPa^{-1}. These data indicate that there was no difference in the conductivities of irrigated roots among RVI treatments, and likewise, conductivities of nonirrigated roots did not vary among RVI treatments. But in all treatments hydraulic conductivity of the nonirrigated roots was less than that of irrigated ones. In other words, there was no difference between treatments in the capacity of irrigated roots to transport water and the lack of soil water reduced the capacity of nonirrigated roots to transport water, regardless of the volume of roots per plant receiving water.

Discussion

A reduction in the irrigated rooting volume of only 25% had a detrimental effect on the performance of young citrus trees grown on a limited volume of soil with low water holding capacity. Fully irrigated plants had higher photosynthetic rates than any of the partially irrigated treatments while plants with only one-quarter of their rooting volume irrigated (1/4 RVI) consistently had the lowest CERs. New leaf and stem growth were also significantly related in a positive, linear fashion to the fraction of rooting volume receiving water. These results agree with the conclusions of most partial irrigation studies of citrus conducted in Florida that any reduction in the soil area or root zone irrigated results in a reduction in tree growth or yield (Koo, 1978; Koo, 1984; Koo, 1985a; Koo and Smajstrla, 1985; Smajstrla and Koo, 1985; Zekri and Parsons, 1988, 1989). Seasonal water-use efficiency was reduced by 8, 37, 43 and 54% in the 3/4, 2/4, 1/4 and 1/4+ RVI treatments, respectively. Thus, in terms of reduction in plant growth with respect to the water that is conserved by partial rooting volume irrigation, the 3/4 RVI treatment was the most advantageous of the partial irrigation treatments and suggests that if partial rooting volume irrigation is used that at least 3/4 of the rooting volume should to be irrigated on sandy soils.

Results of other partial irrigation studies, particularly those conducted on containerized plants with split-root systems, have indicated that the rooting volume receiving water could be reduced to 50% of the total rooting volume without significantly reducing photosynthesis or transpiration over a period of several days (Black and West, 1974; Tan and Buttery, 1982; Tan et al., 1981). A number of studies conducted in Israel, generally on sandy clay loams or heavy clays, have reported variable results, though most indicated that the portion of the root system receiving water could be reduced to some extent while avoiding plant stress. It is interesting to note that, in general, studies which reported detrimental effects on the plant when the rooting volume irrigated was reduced were conducted on sandy soils, whereas those reporting no detrimental effect when a significant portion of the rooting volume was not irrigated were conducted on loamy or clayey soils. This fact suggests that soil hydraulic properties have an important influence on the results of partial rooting volume irrigation studies and may determine the portion of root volume that must be irrigated in order to avoid reductions in growth.

Tan et al., (1981) hypothesized that the favorable performance of plants with only 50% of their rooting volume irrigated was due to an increase in the absorption capacity of the irrigated roots. An alternate explanation may be that the hydraulic resistance of the roots was not the limiting factor and that the increased demand for water uptake by roots as the volume of active roots was reduced was met by greater flow of water in the soil to the roots. The results of this study, as well as those of other partial irrigation studies conducted on sandy soils, may reflect the inability of coarse grained soils with low water holding capacity, rapid drainage, and minimal capillary movement to supply water to roots at a rate adequate to meet the increased demand for water uptake from the irrigated fraction of the soil. But the degree to which water availability for partially irrigated citrus is determined by the soil hydraulic properties alone is not clear nor has it been studied as a single factor influencing the success of partially irrigated plants.

Because of the low water holding capacity and low total volume of the soil used in this study and the rapidity with which CERs decreased, especially during midday, with any apparent decrease in soil water content, it was not possible to discern a difference between irrigation treatments in soil water content at which plant stress was induced. Depletion of ASW resulted in reduced CERs throughout the day but had the greatest effect on CERs during the period of day least affected by atmospheric evaporative demand. But because all trees experienced severe stress and reductions in CERs during a large portion of the day it was not possible to discern appreciable differences between treatments due to the available soil water.

The DBT/DPT controls in this study all resulted in atmospheric vapor pressure deficits greater than 2.0 kPa during the afternoon. Citrus stomatal sensitivity to VPD is well documented in the literature and citrus stomata in the field have been reported to close at VPDs greater than 3.0 kPa (Sinclair and Allen, 1982). It is not possible to determine from the results of this study whether stomata responded primarily to atmospheric or soil water stresses, or in what way these conditions were integrated in the plant. Evapotranspiration rates increased only slightly as evaporative demand increased and support the concept of stomatal regulation of water loss and CO_2 uptake in citrus. But, high leaf temperature which accompanied the conditions of high VPD likely contributed to low photosynthetic rates. Bielorai and Mendel (1969) hypothesized that an increase in mesophyll resistance of citrus leaves as soil water was depleted initiated stomatal closure. The interacting effects of soil and atmospheric water stress on citrus stomatal activity, transpiration, and photosynthesis require further clarification.

Thus, it appears that the response of young citrus trees to partial irrigation in this study were primarily determined by the soil type. The low water holding capacity of builders' sand in conjunction with low capillary movement of water in the soil restricted soil water availability to roots even when the ASW was high. Because of this, plant water stressed developed early in the day as radiation levels rose and was evidenced by severe stomatal closure and midday depression of CERs. Soil or atmospheric moisture conditions appeared to affect CERs at all levels of rooting volume irrigation in a similar manner, i.e., by a reduction of maximum morning photosynthesis and more severe midday depression of photosynthesis as soil water was depleted or vapor pressure deficit increased. The relative influence of soil and atmospheric moisture deficits on the performance of partially irrigated plants may be more discernable in soils with greater water holding characteristics. Due to this behavior it was not possible to fulfill the second objective of the study, i.e., to determine differences in the level of irrigation required to maintain optimum plant growth as water was reduced or as atmospheric evaporative demand was increased.

Water transport per unit length of root did not differ between fully or partially irrigated plants, as shown by hydraulic conductivity measurements. The reduction in plant growth which occurred with reduction in the irrigated root volume is likely due to the inability of the irrigated root volume to supply an adequate amount of water to the plant. Increases in hydraulic conductivity of the irrigated portion of roots does not appear to be an adaptive mechanism of partially irrigated citrus trees. Although this study did not investigate the long term effects and adaptations of citrus trees to partial rooting volume irrigation it is likely that the necessary compensatory increase in water uptake will occur with root regrowth in the irrigated region of the soil. Roots that proliferate beyond the irrigated volume of soil will not contribute to water uptake during periods of irrigation and may result in seasonal stress due to partial rooting volume irrigation.

Future experimental studies should be conducted with the following considerations: higher water holding capacity of the soil; larger rooting volume of compartments; and frequent or continuous replenishment of water in the irrigated compartments of the partial rooting volume study.

CHAPTER V

SIMULATION OF LEAF CONDUCTANCE AND WATER USE OF YOUNG, PARTIALLY IRRIGATED CITRUS TREES

Introduction

Although the results of many partial rooting volume irrigation studies indicate that plant growth and yield are not adversely affected when less than the entire soil volume occupied by the roots is irrigated, this conclusion has not been consistently supported. In addition, the fraction of roots that must be irrigated to avoid reductions in growth, yield or water use, varies greatly between studies. Results of partial-rooting-volume irrigation studies fall into two categories: those which indicate that a large reduction in the portion of roots irrigated does not have detrimental effects on photosynthesis, transpiration, growth, or yield (Black and West, 1974; Tan and Buttery, 1982; Tan et al., 1982; Bielorai et al., 1981), and those which indicate that these processes are significantly reduced as the portion of irrigated rooting-volume is reduced (Koo, 1978; Smajstrla and Koo, 1985; Zekri and Parson, 1988, 1989, see also chapter IV). Thus, general statements concerning the effects of partial-rooting-volume irrigation are difficult to make.

It was hypothesized that soil type, atmospheric evaporative demand, and root length density are major determinants of the capacity of partial-rooting-volume irrigation practices to supply sufficient water to the crop. To test this hypothesis the model WATFLW (Water Flow) was developed which describes water use of young citrus trees with all or only a portion of their root system irrigated and was used to investigate the manner in which soil type, root length density, and atmospheric evaporative demand influence the portion of the root system that must be irrigated to meet plant water requirements.

General Description

WATFLW describes the stomatal behavior and water use of a young citrus tree with all or various fractions of its root system irrigated. Solar radiation, dry-bulb temperature, and dewpoint temperature are inputs to the system, which consists of a single, entire, citrus tree, bounded by the outer radius of the root-occupied soil volume and by the atmosphere at a distance well beyond the leaf boundary layer. Transpiration is calculated as the absolute humidity difference between the leaf and air times the leaf conductance. All leaves of the young canopy are considered to receive equal irradiance so that transpiration rate was multiplied by the total leaf area to obtain the 'demand' for water. Extraction of soil water is described using a microscopic-scale approach which considers the radial flow of water to individual roots. This approach describes a cylindrical shell of soil that surrounds each root and is divided into a specified number of concentric cylindrical compartments. The volumetric rate of water loss from the shoot also represents the rate of water extraction from the first concentric compartment around the roots. Subsequently, water redistribution rates in the soil are determined by the water potential difference and average hydraulic conductivity of contiguous cylinders. Stomatal activity provides the regulatory mechanism of the plant for controlling water loss in response to solar radiation, atmospheric evaporative demand, and soil water status in the immediate vicinity of the roots. An important assumption of the model is that stomata respond to the water potential of the soil in contact with the roots rather than to leaf water potential. For this reason hydraulic resistances in the plant were not estimated.

Entire or partial rooting volume irrigation is effected by dividing the rooting volume into a specified number of sections identical with respect to volume, soil type, and root length density. Four sections were used for this study and are referred to here as the soil quadrants. Partial irrigation of the root system is effected by specifying the initial volumetric water content (θ) of each quadrant. Irrigated quadrants are assigned an initial θ value equal to field capacity while nonirrigated quadrants are assigned an initial θ value equal to wilting point. No water flow occurs between separate quadrants. This assumption is reasonable in the case of coarse grained soils but lateral flow of water between irrigated and nonirrigated regions should be accounted for on heavier soils. The model is equipped with an option for irrigating various quadrants of the rooting volume at a specified level of soil water potential or volumetric water content.

Model Development

A component diagram of the primary processes and variables in the model WATFLW is shown in Figure 5.1 and a computer program flow chart of

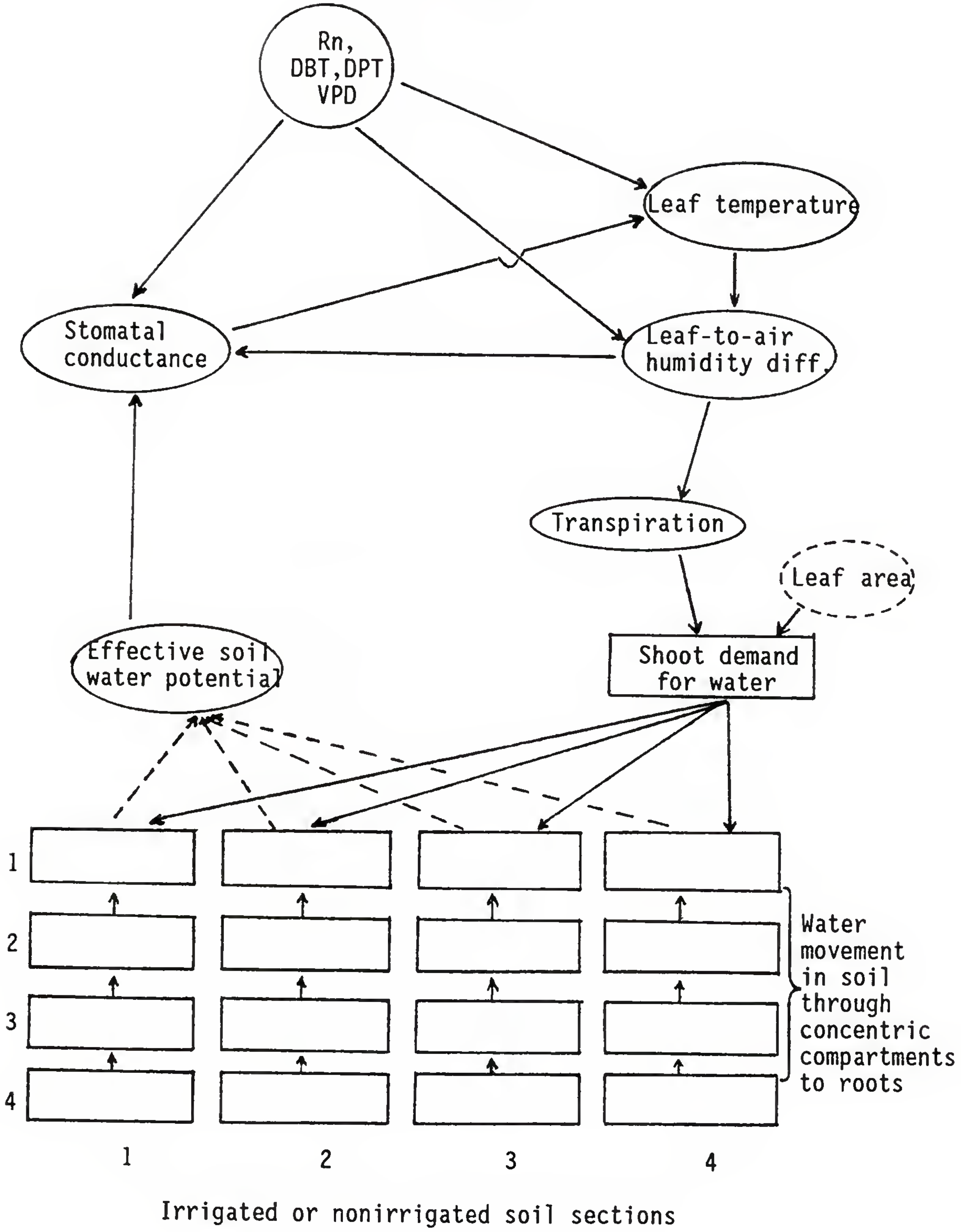

Rn,
DBT,DPT
VPD
Leaf temperature
Stomatal conductance
Leaf-to-air humidity diff.
Transpiration
Leaf area
Effective soil water potential
Shoot demand for water
1
2
3
4
Water movement in soil through concentric compartments to roots
1
2
3
4
Irrigated or nonirrigated soil sections

Figure 5.1 Component diagram of WATFLW, a model of water use by a citrus tree.

the model is included in Appendix E. WATFLW was written in FORTRAN and run on the IBM mainframe computer at the Northeast Regional Data Center, as well as on the SUN computer and personal computers in the Agricultural Engineering Department, University of Florida, Gainesville. The FORTRAN source code for WATFLW is included in Appendix F. Soil, plant, and time parameter values are read from an input file. Photosynthetically active radiation, dry-bulb temperatures, and dewpoint temperatures are also read an input file at five-minute intervals of simulated time; values at intermediate time steps are calculated by linear interpolation. Initially the model calculates the dimensions of the soil quadrants and the concentric compartments surrounding the roots. Energy balance equations are solved in the dynamic portion of the model to determine leaf temperature. Stomatal conductance, transpiration rate and the volumetric shoot water loss are calculated next. Soil water flow equations are solved in the subroutine WATFLW. The function TLULIN uses a table of soil water release data for calculating soil water potential by linear interpolation of the volumetric water content values. The change in the volumetric water content of each compartment is calculated using Runge-Kutta fourth order integration in the subroutine INTEGR. The subroutine DEL calculates a variable time step using the criteria of the maximum allowable change in volumetric water content of a compartment; for the present study constant time steps were specified. A time step of 1.0 second was specified for simulations on Parkwood variant fine sandy loam and 0.1 second was the time step used for simulations on Astatula fine sand.

Water Movement in the Soil to the Roots

The sandy nature of many soils on which citrus is grown in Florida, as well as the low root-length density of citrus, are conditions conducive to the development of large soil water content gradients in the vicinity of plant roots (Philip, 1957; Gardner, 1960; Passioura, 1988). For this reason a microscopic-scale approach to modeling soil water movement was adopted. The soil water flow model developed by Hillel et al., (1975) and written in IBM S/360 CSMP computes the radial movement of water and noninteracting solutes to plant roots. WATFLW incorporates the soil water flow component of the model by Hillel et al. (1975) with several modifications.

The soil volume considered in WATFLW can be envisioned as a cylinder of soil of radius equal to that of the ground surface area wetted by the irrigation system, or to the distance from the tree trunk to which roots are known to extend, and of depth equal to the soil depth wherein most roots are found or most water from irrigation penetrates. Within each quadrant of the soil roots are uniformly distributed and each root is assumed to be surrounded by a cylindrical volume of soil. The radius of the cylindrical volume of soil surrounding each root is determined from the root-length within a cubic centimeter of soil, or the root-length density: the greater the root-length density, the smaller the radius of the cylindrical volume of soil. In turn, the cylindrical volume of soil is divided into a specified number of concentric cylindrical shell compartments, (K). The thickness of the first cylindrical shell soil compartment (adjacent to the root) is computed using arbitrary values for the relative increase in thickness of the cylindrical shell compartments and the number of cylindrical shell compartments into which the whole cylindrical volume is divided. From this, the peripheral area of the root, the radial flow distance, and volume of the first cylindrical shell soil compartment can be calculated. Subsequently, the thickness, radius, peripheral area, and radial flow distance of the remaining cylindrical shell compartments are calculated.

WATFLW calculates water extraction from the first cylindrical shell soil compartment as:

$$FLW(L,1) = FLFAC(L,1) * TRAN \tag{5.1}$$

where,

FLFAC(L,J) = a root-length density and soil hydraulic conductivity weighted factor for each soil quadrant equal to

$$FLFAC(L,1) = RLD(L) * TOTCOND(L)/TOTFAC,$$

RLD(L) being the root-length density in quadrant L and TOTCOND is the sum of the hydraulic conductivities of the concentric compartments in the quadrant (L). TOTFAC is the sum of the product of RLD * TOTCOND for all soil quadrants.

TRAN = the volumetric rate of water loss from the shoot and is defined in a separate section.

Using this method, a greater portion of the total transpiration will be extracted from the quadrant having a higher root-length density or higher hydraulic conductivity. As the hydraulic conductivity of a particular quadrant decreases, water extraction shifts towards the quadrant with higher hydraulic conductivity, which also represents higher soil water content. A similar soil hydraulic conductivity and root-length density weighted method of calculating water extraction from different soil layers was utilized by Slack (1977).

Initially, uniform soil water conditions exist throughout each quadrant. During the first time step water is extracted from the first cylindrical shell compartment of irrigated quadrants. During the next time step the volumetric water content of each cylindrical shell compartment is computed and used to determine the soil water potential by linear interpolation of soil water release curve data. WATFLW calculates the hydraulic conductivity of each cylindrical shell compartment as a function of soil water potential using Van Genuchten's (1980) equation

$$K(\psi) = \frac{K_s \{1 - (x \psi)^{n-1} [1 + (x \psi)^{n}]^{-m}\}^2}{[1 + (x \psi)^{n}]^{m/2}} \tag{5.2}$$

where

ψ = soil matric potential, cm water,

K = unsaturated hydraulic conductivity of the soil as a function of ψ, cm s^{-1},

K_s = saturated hydraulic conductivity of the soil, cm s^{-1},

x, n = parameters estimated using nonlinear regression,

$m = 1 - 1/n$.

A table of variable definitions is included in Appendix G.

Water flow rates are computed in WATFLW, as in the model by Hillel et al. (1975) using the general flow equation in the form

$$FLW(L,J) = COND(L,J) * (POTGD(L,J)/DR(L,J)) * AREA(L,J) \tag{5.3}$$

where

FLW(L,J) = the volumetric rate of water flow ($cm^3 s^{-1}$), from quadrant L, cylindrical shell compartment J to cylindrical shell compartment J-1 of the same quadrant,

COND(L,J) = the mean hydraulic conductivity ($cm s^{-1}$) of cylindrical shell compartments (L,J) and (L,J-1),

POTGD(L,J) = the soil water potential (cm water) difference between cylindrical shell compartments (L,J) and (L,J-1),

DR(L,J) = the radial length (cm) of flow for each cylindrical shell compartment, calculated as the distance between midpoints of adjacent cylindrical shell compartments,

AREA(L,J) = the peripheral area of cylindrical shell compartment (L,J) that is in contact with compartment (L,J-1), (cm^2).

The initial dimensions of the total root occupied soil, 30 cm in diameter and 45 cm deep, described a cylinder of soil with a volume of 31.8 L, approximately equal to the total volume of the split-root containers (30 L) used in the partial irrigation study in 1986. Subsequently, the diameter of the irrigated soil volume was changed to 60 cm, a value representative of the irrigated area of soil for young, field-grown citrus trees, which was about four times the total rooting volume of the split-root containers described in Chapter IV.

Initially, water extraction patterns of fully irrigated citrus on builders' sand was simulated. Subsequently, two Florida soils were used: Astatula fine sand (Typic Quartzipsamment, hyperthermic, uncoated), a common soil type on many citrus planting sites in Florida, and Parkwood variant fine sandy loam (Mollic Ochraqualfs, fine-loamy, mixed, hyperthermic). The soil moisture release curve for builders' sand was measured in the Soil Characterization Lab, University of Florida, Gainesville, and water release data and hydraulic properties of the Astatula fine sand and Parkwood fine sandy loam were obtained from Florida soil characterization reports (Carlisle et al., 1978). Water release curves for the three soil types are shown in Figure 5.2. Parameters for Van Genuchten's equation for hydraulic conductivity for the three soil types are given in Appendix H. Varying the soil type resulted in changes in the water holding and conducting ability of the soil.

The Atmosphere

Five-minute photosynthetically active radiation (PAR, μmol m^{-2} s^{-1}), dry-bulb temperature (DBT, °C), and dewpoint temperature (DPT, °C) data collected in the soil-plant-atmosphere (SPAR) chambers at the Irrigation Research and Education Park, University of Florida, Gainesville, during the summer of 1986, were used as inputs to the model. Net radiation (Rn) was calculated from photosynthetic radiation data using a factor of 4.57 μmol (photon) m^{-2} s^{-1} per W m^{-2} (Thimijan and Heins, 1983) to first convert incident PAR in the chambers to energy units. Since PAR represents about 47% of the energy of solar radiation, incident total solar energy can be obtained by dividing incident PAR energy by 0.47. According to Table 2.3 of Jones (1983), leaf net radiation represents about 48% of the total solar irradiance on a sunny day. Thus, the

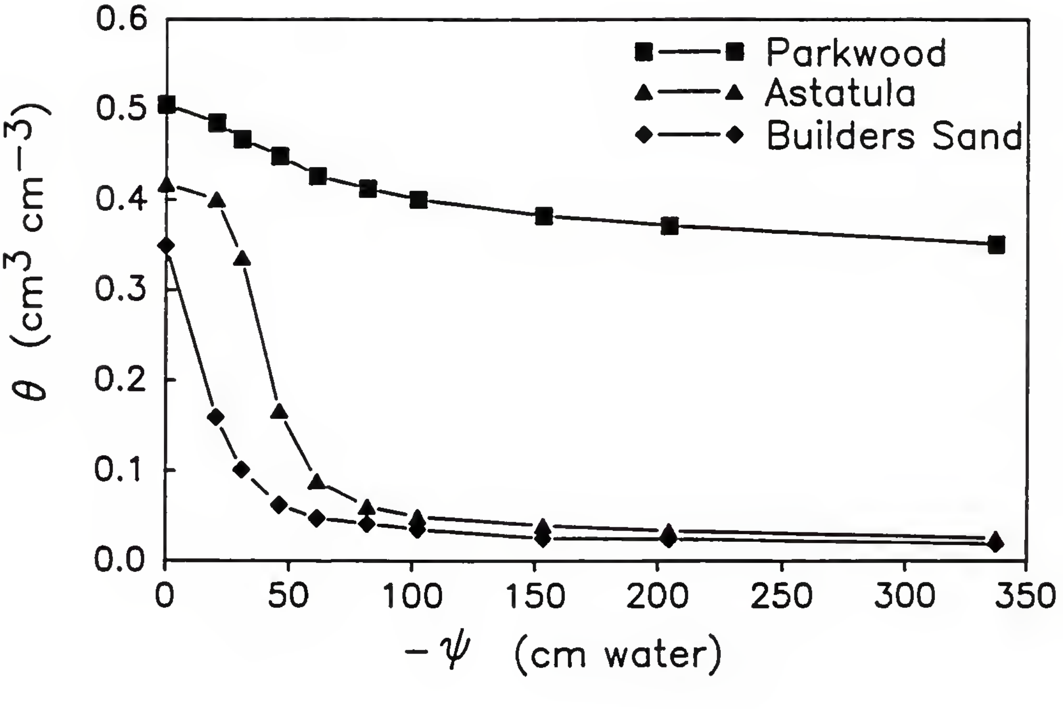


Figure 5.2 Relationship between volumetric water content (θ) and soil water potential (ψ) for three soil types used in simulations of citrus water use. Water release data for Astatula fine sand and Parkwood variant fine sandy loam were obtained from the Florida Soil Characterization Report (Carlisle, 1978).

factors 0.48/0.47 cancel. Therefore, for convenience in simulations Rn was simply calculated by dividing PAR in the chambers by 4.57 μmol (photon) m^{-2} s^{-1} per W m^{-2}. This calculation would tend to overestimate Rn at low values of PAR, such as near the beginning and ending of the day, and underestimate Rn under cloudy conditions. Environmental data (Figures 5.3 - 5.5) within the SPAR chambers for 30 July 1986 were chosen for the high DBT/VPD treatment because of high radiation during the day with only intermittent periods of cloudiness (See Chapter IV for a complete discussion of experimental conditions). Low radiation during the day on 28 August 1986, resulted in reduced dry-bulb temperatures in the chambers. Environmental data for this day were selected for the low DBT/VPD treatment. Between 2000 and 0600 EST on both 30 July and 28 August, constant solar radiation of 0.1 μmol m^{-2} s^{-1}, and dry-bulb and dewpoint temperatures of 24 and 18 °C, respectively, were specified. The same set of environmental data for either the high DBT/VPD or low DBT/VPD condition was used for each day of the simulation. Absolute humidity of the air and atmospheric saturation vapor pressure deficit were calculated from dry-bulb and dewpoint temperatures.

Initially, leaf temperature is set approximately equal to the dry-bulb temperature at 0600 EST. This estimation is used to calculate saturation vapor pressure of water at leaf temperature. Leaf resistance is assigned an initial value of half the cuticular resistance. Leaf temperature and leaf resistance attained nearly constant values, which were relatively unaffected by their initial values, within the first several seconds of simulation. Leaf temperature is calculated using an energy balance equation of the following form (Idso et al., 1986)

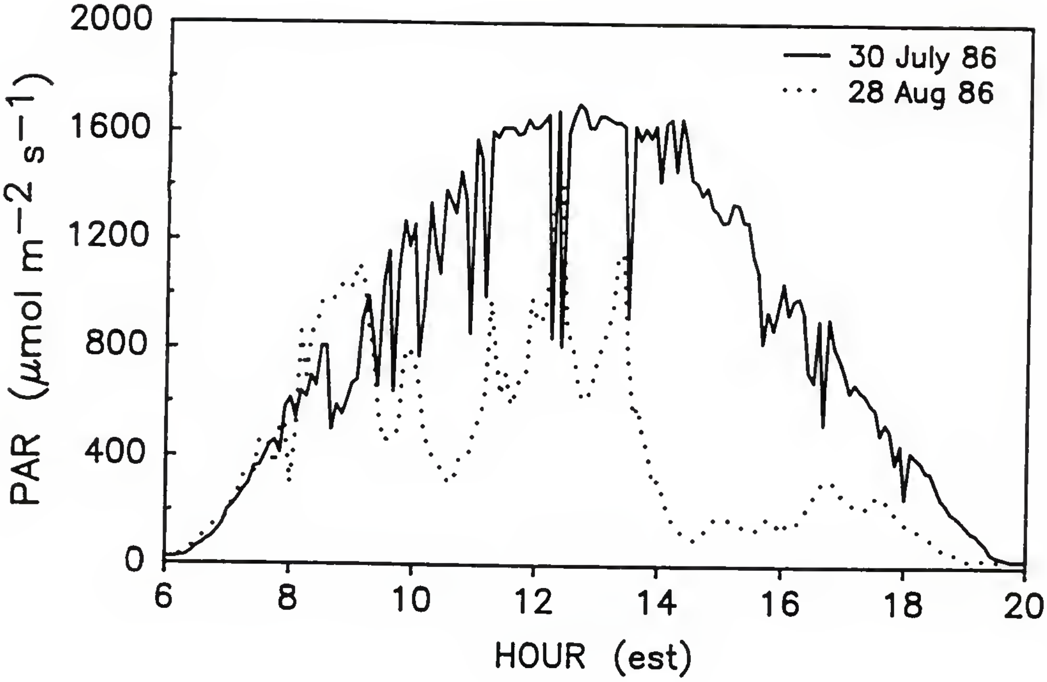


Figure 5.3 Diurnal photosynthetically active radiation (PAR) in the soil-plant-atmosphere-chambers on two days during a study of partial irrigation of citrus trees.

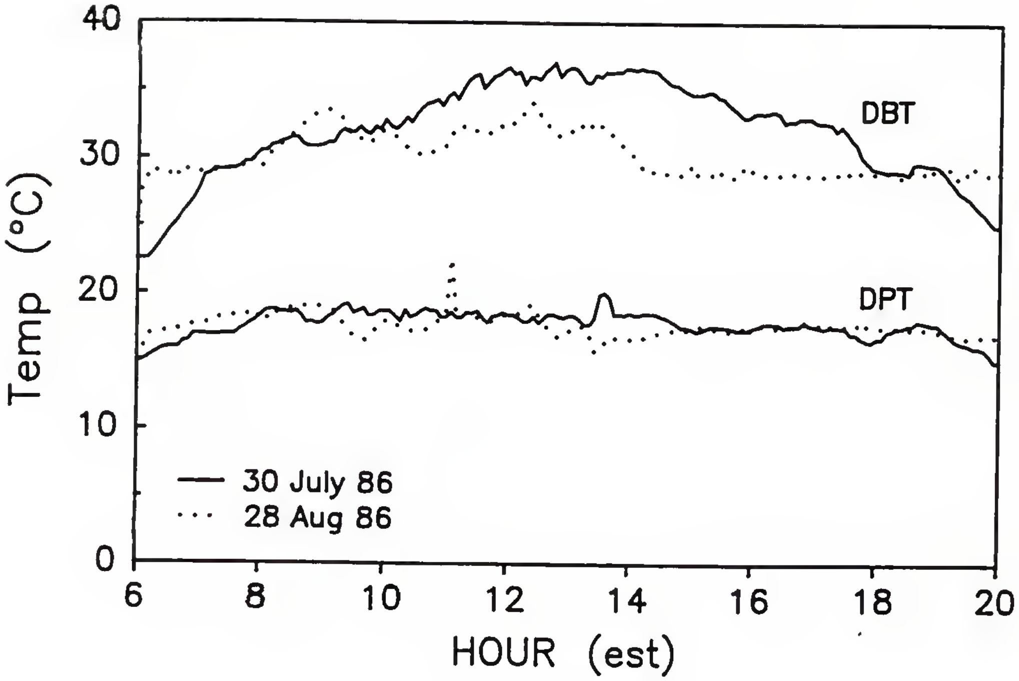


Figure 5.4 Diurnal dry-bulb and dewpoint temperatures (DBT and DPT, respectively) in the soil-plant-atmosphere chambers on two days during a study of partial irrigation of citrus trees.

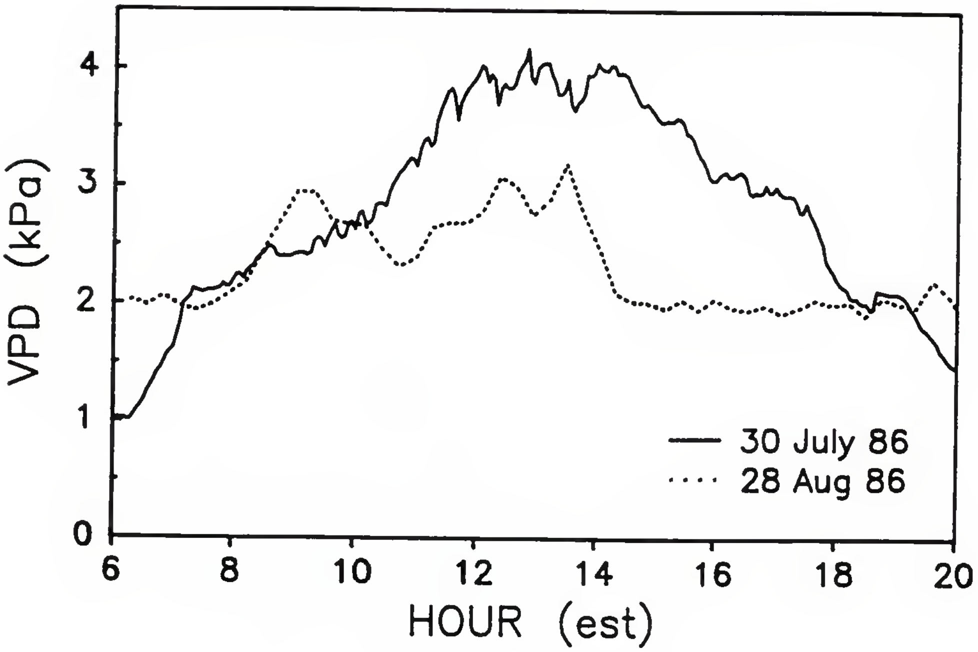


Figure 5.5 Diurnal atmospheric water vapor pressure deficit (VPD) in the soil-plant-atmosphere chambers on two days during a study of partial irrigation of citrus.

$$T_L = T_A + \frac{r_a R_n}{\rho C_p} \cdot \frac{\gamma^*}{\Delta + \gamma^*} - \frac{VPD}{\Delta + \gamma^*} \qquad (5.4)$$

where

T_L = temperature of the leaf, °C,

T_A = temperature of the air, °C,

R_n = net radiation, W m^{-2},

r_a = aerodynamic resistance to water vapor transport between the leaf surface and the air in s m^{-1}, calculated as (Jones, 1986)

$$0.9(1./(6.62(u/d)^{0.5}))\cdot 1000$$

where

u = velocity of wind, set to a constant value of 1.5 m s^{-1}, the value measured in the SPAR chambers.

d = leaf width, set to 0.06 m, a representative value for citrus leaves.

0.9 = the ratio of diffusivity of heat to diffusivity of water vapor, raised to the 2/3 power (Thom, 1968).

The resulting constant value of r_a was 27.2 s m^{-1}.

ρ = density of air, kg m^{-3},

C_p = heat capacity of the air, J kg^{-1} °C^{-1},

Δ = slope of the saturated vapor pressure-temperature relation evaluated at leaf temperature, kPa °C^{-1},

VPD = air vapor pressure deficit, kPa,

γ = psychrometric constant, kPa °C^{-1},

$\gamma^* = \gamma(1 + r_s/r_a)$,

r_s = leaf resistance to water vapor transport, s m^{-1}.

This equation is solved iteratively. Saturation water vapor pressure at leaf temperature is then recalculated using the calculated value of leaf temperature and used to determine the leaf-to-air absolute humidity difference (g m^{-3}), the driving force for water vapor loss from the leaves.

The Plant

The primary plant factors influencing water availability and uptake in WATFLW are leaf area, root-length density, and stomatal conductance. Leaf area was specified as 5000 cm^2 and did not change during the simulation. This represents the average leaf area of fully irrigated citrus trees in the 1986 study (Chapter IV). In the approach used, all leaves are considered to receive equal irradiance. Root-length density was initially set to 0.12 cm cm^{-3} and likewise was the mean of values calculated for fully irrigated citrus trees growing in split-root containers in 1986. Root-length density was subsequently changed to 1.0 cm cm^{-3}, a value well within the range of reported values of root length density for citrus (Mikhail and El-Zeftawi, 1980; Bevington and Castle, 1982; Marler, 1988), to determine the degree to which this parameter influences water use of fully and partially irrigated citrus trees. The model assumes that the effective absorbing root length is equivalent to the entire root length.

At each time step of the model, water loss from the shoot is calculated from the transpiration rate multiplied by the total leaf area, and this amount is extracted from the cylindrical compartment adjacent to the roots. The ratio of leaf area to root length is therefore an indication of the relative magnitude of water flux per unit root length, q. The soil water content and potential difference between the root surface (r_1) and a radial distance (r_2) from the root under steady-state flow is directly proportional to q, as indicated in the equation for radial flow of water towards the central axis of a cylinder (2.14)

$$\psi_1 - \psi_2 = \frac{q}{4\pi K} \ln(r^2_2/r^2_1)$$

Initial values of leaf area, root-length density, and soil volume used in simulations resulted in a leaf area/root length ratio similar to that found for fully irrigated citrus in the partial irrigation study in 1986. The subsequent increase in root-length density resulted in a decrease in this ratio, hence a decrease in water flux per unit root length.

In order to develop an expression of leaf conductance as a function of radiation, leaf-to-air humidity difference, and soil water status, published results of citrus leaf conductance studies were reviewed. Although many studies have been conducted on leaf conductance response to individual or complementary environmental variables, such as temperature and humidity deficit, the effect of interactions among several factors has received little attention. The initial approach to calculating leaf conductance incorporated an equation described by Shawcroft (1971) for leaf resistance of corn as a function of radiation

$$r_s = a + \frac{b}{(I + I_o)} \qquad (5.5)$$

where

r_s = leaf resistance,

I = photosynthetically active radiation, PAR

I_o = minimum solar radiation parameter, required to avoid infinite r_s as I approaches zero, which helps to define cuticular resistance,

a = asymptotic minimum leaf resistance at high light,

b = $x \circ y$ hyperbolic constant $[=(r_s - a)(I + I_o)]$.

Rearranging, leaf conductance (g_s) can be written as

$$g_s = \frac{(I + I_o)}{(I + I_o)a + b} \qquad (5.6)$$

Data relating leaf conductance to photosynthetically active radiation were extracted from reports by Hall et al. (1975) and Kriedemann (1971). Nonlinear regression was used to fit these data to equation (5.6) and obtain values for I_o, a, and b. A family of leaf conductance curves as a function of radiation at varying levels of leaf-to-air absolute humidity deficit (AHDF) can be generated by calculating a as the leaf conductance value as a function of AHDF while holding b constant. Data relating citrus leaf conductance to the leaf-to-humidity difference were obtained from: Khairi and Hall (1976a,b); Kaufmann and Levy (1976); Hall et al. (1975); and Levy (1980). Nonlinear regression was used to fit these data to an equation of the form

$$\frac{1}{a} = c + \frac{d}{AHDF + z} \qquad (5.7)$$

where

$1/a = G_s$ = maximum leaf conductance at high solar radiation, made a function of AHDF, ie., $G_s(AHDF)$,

c = the asymptotic minimum value of $G_s(AHDF)$ as absolute humidity difference is increased,

z = the offset on the horizontal axis required to avoid infinite resistance when AHDF equals zero.

The effect of soil water potential was incorporated into equation (5.7) using the factor, SP/SPREF, where SP is the mean soil water potential of the first cylindrical compartment in all soil layers and SPREF is the reference soil water potential of the particular soil. The final equation for a, which essentially represents leaf conductance as a function of the leaf-to-air absolute humidity difference and soil water potential was

$$\frac{1}{a} = \left(c + \frac{d}{AHDF + z}\right) \cdot \frac{SP}{SPREF} \qquad (5.8)$$

Diurnal values of leaf conductance estimated using equations (5.6) and (5.8) are shown in Figure 5.6. Although this approach gave reasonable predictions of leaf conductance response to radiation and absolute humidity deficits, the response to soil water potential was not based on an experimentally determined relationship and results were not

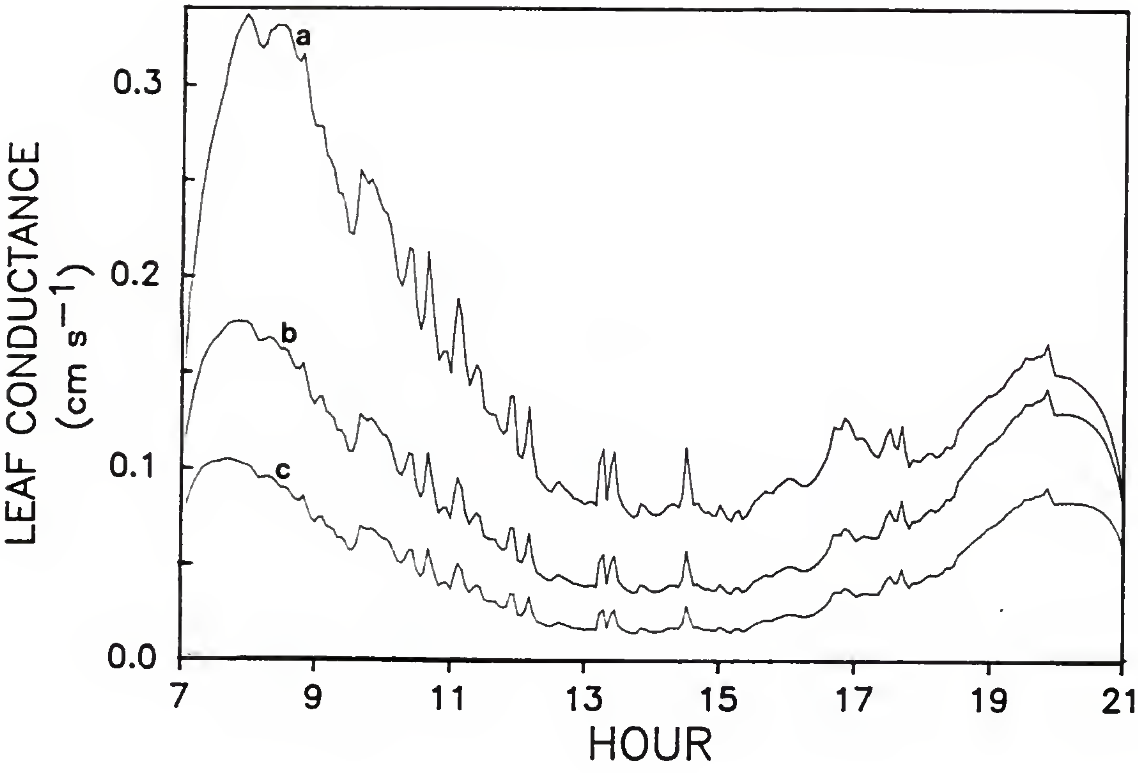


Figure 5.6 Simulated leaf conductance calculated with equation (5.7) using three values of z (the horizontal offset to avoid infinite resistance at a humidity deficit of zero): a) z = 3, b) z = 5, c) z =10. Data are for fully irrigated citrus trees on Astatula fine sand using weather data from the soil-plant-atmosphere chambers on 30 July 1986.

satisfactory with respect to this variable. This approach should work if a functional equation or table of values relating leaf resistance (or leaf conductance) to soil water potential were derived and used in place of SP/SPREF. For example, a functional relationship factor such as $r_s(SP)/r_s(SPREF)$ could be used, where r_s would be determined from the variable SP and the fixed value of SPREF.

Even with a functional response of leaf conductance to soil water potential, equations (5.6) to (5.8) would be awkward to use, so an alternate approach was derived and found to give satisfactory results. The alternate approach permitted direct combination of the three separate functions of leaf conductance to solar radiation, absolute humidity deficit, and soil water potential as a series of multiplicative factors. In other words, $g_s = g_s(PAR, AHDF, SP)$ was assembled as a product of g_s as a function of each separate factor, i.e., $g_s(PAR, AHDF, SP) = g_s(PAR) \cdot g_s(AHDF) \cdot g_s(SP)$. This approach assumes that the individual relationships between leaf conductance and solar radiation, absolute humidity difference, and soil water potential extracted from data in the literature lie on the same response surface and do not interact in a synergistic manner. Using an assumption of the level of humidity deficit at which the relationship between leaf conductance and radiation was obtained, the two separate functions could be combined as multiplicative factors. In a similar manner, soil water potential was combined with the expression for leaf conductance as a function of the radiation and humidity deficit. Leaf conductance response to radiation was described using a hyperbolic equation of the form

$$g_s = \frac{I \ G_s}{I + K_m} \tag{5.9}$$

and fit to the relationship between leaf conductance and solar radiation obtained from nonlinear regression of data reported in the literature (Figure 5.7). This equation is essentially the same as equation (5.6) where $G_s = 1/a$, $K_m = b/a$, and I_o is ignored. Combination of the three separate functions was facilitated by using equation (5.9).

Leaf conductance at high light as a function of absolute humidity deficit, $g_s(\mathrm{AHDF})$, was calculated using the equation

$$g_s(\mathrm{AHDF}) = \frac{h}{\mathrm{AHDF} + w} \tag{5.10}$$

where h and w are parameters determined using nonlinear regression. Data on leaf conductance as a function of leaf-to-air humidity deficit reported in the literature were fit to equation (5.10) (Figure 5.8). Equation (5.10) was combined with equation (5.9) by evaluating equation (5.10) at an absolute humidity deficit value of 5 g m^{-3}, the value at which the relationship between leaf conductance and solar radiation data were obtained. Then G_s of equation (5.9) was weighted by the ratio $g_s(\mathrm{AHDF})/g_s(\mathrm{AHDF}_5)$. For convenience in subsequent steps, G_s weighted for leaf-to-air humidity deficit, $G_s(I,\mathrm{AHDF})$, can be written in terms of a factor C' as:

$$G_s(I,\mathrm{AHDF}) = G_s \cdot g_s(\mathrm{AHDF})/g_s(\mathrm{AHDF}_5) = g_s(\mathrm{AHDF}) \cdot C' \tag{5.11}$$

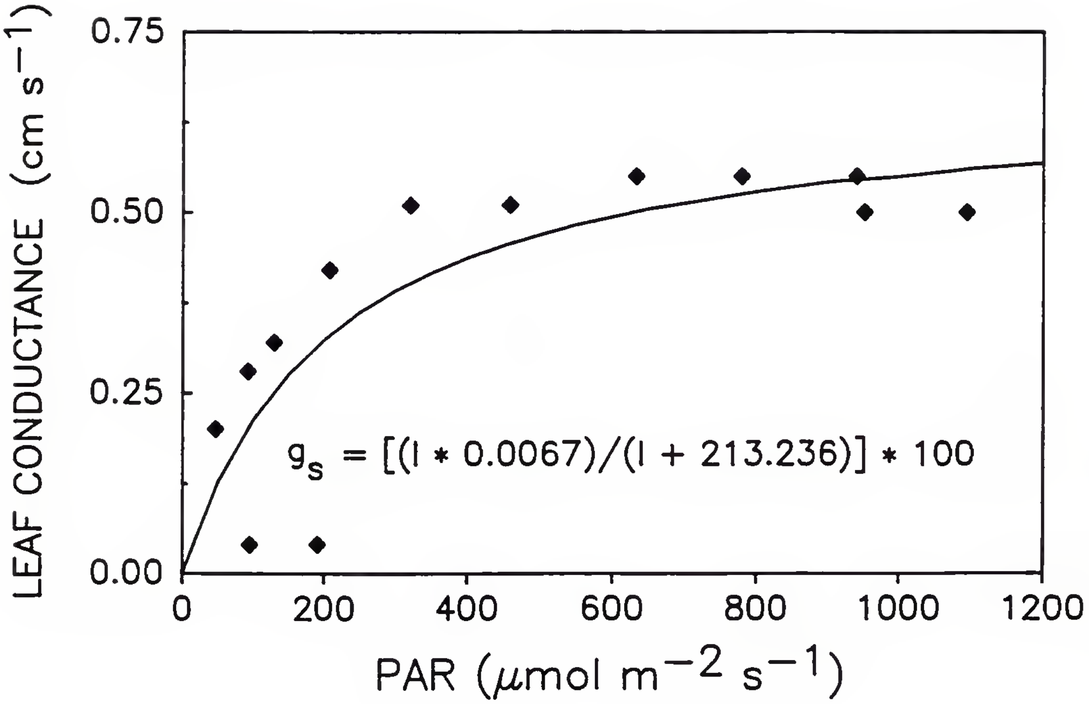


Figure 5.7 The functional relationship between stomatal conductance of citrus and photosynthetically active radiation (PAR) derived from data of Hall et al., (1975) and Kriedemann (1971).

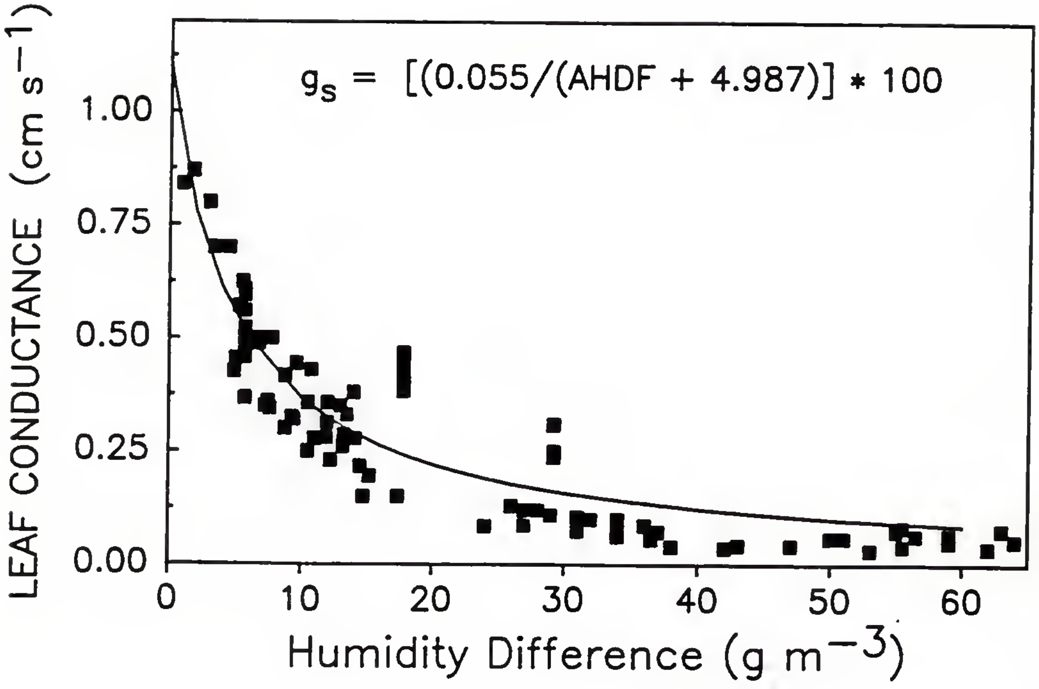


Figure 5.8 The functional relationship between the stomatal conductance of citrus and the leaf-to-air absolute humidity difference (AHDF) derived from data of Khairi and Hall (1976 a,b), Kaufmann and Levy (1976), Hall et al., (1975), and Levy (1980).

where C' is defined as

$$C' = \frac{G_s}{g_s(AHDF_5)} = G_s \cdot [h/(5.0 + w)]^{-1} \qquad (5.12)$$

Thus, leaf conductance as a function of radiation and absolute humidity was described by the equation

$$g_s = \frac{I}{I + K_m} \cdot \frac{h}{AHDF + w} \cdot C' \qquad (5.13)$$

Only a single reference (Stanhill, 1978) was found expressing a relationship between citrus canopy resistance and soil water potential. Estimates of unit leaf stomatal conductance were obtained by taking the reciprocal of canopy resistance, multiplied by an estimated value of leaf area index of five, as a function of soil water potential. The scarcity of data available in this area emphasizes the lack of understanding of how citrus stomatal activity relates to soil water status. Leaf conductance as a function of soil water potential $g_s(WP)$ was described using a hyperbolic equation of the form

$$g_s(WP) = \{[g_{s(max)} - g_{s(min)}] / (p^{-1} \cdot WP + 1)\} + g_{s(min)} \qquad (5.14)$$

where

$g_{s(max)}$ = the maximum value of leaf conductance, fixed at 0.8 cm s^{-1}, based on the relationship between g_s and soil water potential obtained from data of Stanhill (1978),

$g_{s(min)}$ = the minimum value of leaf conductance, fixed at 0.0006 cm s^{-1}, based on the relationship between g_s and soil water potential data obtained from the same source, WP = a calculated factor for the effective soil water potential, expressed as the negative value of cm of soil water suction.

Values of $g_{s(max)}$ and $g_{s(min)}$ specify the y intercept and the horizontal asymptote values, respectively. The value of p^{-1}, which determines the slope of the vertical arm of the curve, was determined by fitting the data of Stanhill (1978) to equation (5.14) using nonlinear regression (Figure 5.9). The least squares estimate of p was 441 cm water using these data and subsequently was specified so as to yield a leaf conductance close to cuticular conductance at the predetermined level of wilting point for the soils used in the simulation. Thus, p was reduced to 300 cm water for simulations of citrus leaf conductance on the Astatula fine sand and Parkwood variant fine sandy loam.

The factor WP in equation (5.14) represents the effective soil water potential and was calculated as the water potential of the average volumetric water content in the cylindrical compartments closest to the roots in all quadrants and includes a factor to account for plant water storage. The purpose of the water storage factor is to delay leaf conductance response to changes in soil water potential by a constant factor until the average volumetric water content of the first compartment in the quadrants reaches the volumetric water content at wilting point (WPT).

The volumetric water content at wilting point was specified for each soil and represents the water content where soil hydraulic conductivity was negligible and nearly equal in both soils. The value of the average volumetric water content in the soil closest to the roots was then increased by a factor (FAC) calculated as the difference

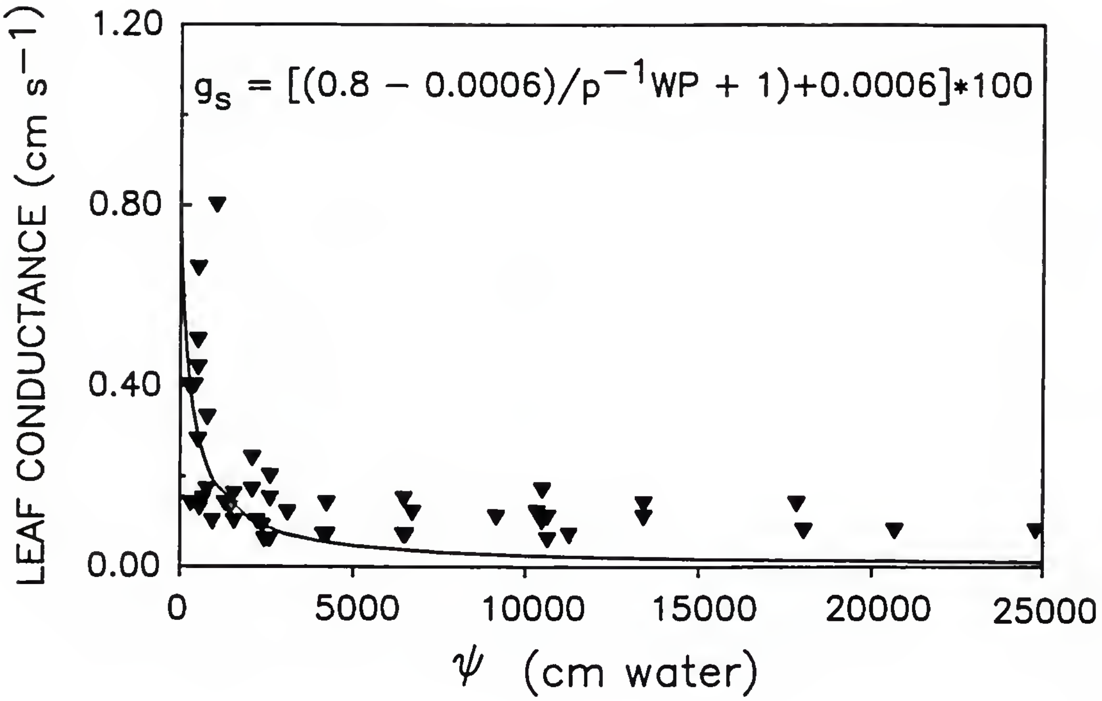


Figure 5.9 The functional relationship between stomatal conductance and soil water potential of citrus trees derived from data of Stanhill (1978).

between volumetric water content at field capacity (θ_{FC}) and volumetric water content at the wilting point (θ_{WPT}) times the ratio of the maximum amount of water in a young citrus tree at full hydration, TPLW (cm^3), to water in the soil volume at field capacity, TSW (cm^3),

$$FAC = (\theta_{FC} - \theta_{WPT}) \cdot (TPLW/TSW) \qquad (5.15)$$

The water content of a fully irrigated, young citrus tree was estimated using fresh and oven-dry weight differences of leaves and stems of the fully irrigated citrus trees from the 1986 study, a representative value being 1600 cm^3 per plant. Total water in the soil represents θ_{FC} times the total soil volume. In this way the average volumetric water content of the cylindrical compartments in contact with the roots was increased by the same amount on both soils. The value of FAC calculated as such was very small and did not have a large effect on stomatal response to the effective soil water potential.

When the average volumetric water content of the soil reaches the value at wilting point, water remaining in the soil is considered to be unavailable to the plant. At this point the constant representing plant water storage is reduced by a factor representing the relative water content of the plant (RPLW) or, the ratio of plant water (PLW) to maximum plant water (TPLW). Plant water was calculated in the model by subtracting from the total plant water the volume of water transpired at each time step. When RPLW reached 25 percent the plant was considered to be dead and the simulation was terminated. Thus, WP is determined in the following manner

$$WP = \psi[\bar{\theta} + (\theta_{FC} - \theta_{WPT}) \cdot FAC], \qquad \text{when } \bar{\theta} > WPT \qquad (5.16)$$

and

$$WP = \psi[\bar{\theta} + (\theta_{FC} - \theta_{WPT}) \cdot FAC \cdot RPLW], \quad \text{when } \bar{\theta} < WPT \tag{5.17}$$

where $\bar{\theta}$ is the average water content of the first compartment surrounding the roots in all quadrants.

Equations (5.13) and (5.14) were combined in a manner similar to the combination of equations (5.9) and (5.10) by evaluating equation (5.13) at a value of 10 cm, the assumed level of soil water potential at which the data describing stomatal conductance as a function of radiation and as a function of leaf-to-air humidity difference were collected. The value of G_s of equation (5.9) was weighted again by the ratio $g_s(WP)/g_s(WP_{10})$ applied to $G_s(I,AHDF)$ of equation (5.11).

$$\begin{aligned} G_s(I,AHDF,WP) &= g_s(AHDF) \cdot g_s(WP)/g_s(WP_{10}) \cdot C'' \\ &= g_s(AHDF) \cdot g_s(WP) \cdot C'' \end{aligned} \tag{5.18}$$

where C'' is defined as

$$C'' = \frac{C'}{g_s(WP_{10})} =$$

$$C' \cdot \left(\frac{g_{s(max)}(WP) - g_{s(min)}(WP)}{(10 \cdot P^{-1} + 1) + g_{s(min)}(WP)} \right)^{-1} \tag{5.19}$$

The final equation describing leaf conductance as a function of radiation, leaf-to-air humidity difference, and soil water potential with a factor to delay leaf conductance response to soil water potential was

$$g_s = \frac{I}{I + K_m} \cdot \frac{1}{AHDF + w} \cdot \left(\frac{g_{s(max)} - g_{s(min)}}{p^{-1} \cdot WP + 1} + g_{smin} \right) \cdot C'' \tag{5.20}$$

Thus, equation (5.20) is the derived operational relationship of leaf conductance as a function of I, AHDF, and WP

$$g_s = G_s(I) \cdot \frac{g_s(AHDF)}{g_s(AHDF_5)} \cdot \frac{g_s(WP)}{g_s(WP_{10})} \qquad (5.21)$$

The diurnal pattern of citrus leaf conductance on Astatula fine sand calculated using equation 5.20 and weather data from 30 July 1986 in the SPAR chambers is shown in Figure 5.10. This diurnal response of citrus leaf conductance is similar in shape to diurnal patterns of citrus leaf conductance reported by Meyers and Green (1981), Zekri (1984), and Marler (1988).

Since I_o of equation (5.6) and c of equation (5.7) were deleted in equation (5.9) and subsequently in the derivation of equation (5.20), leaf conductance will approach zero as solar radiation approaches zero or as AHDF gets very large. However, the functions performed satisfactorily because they made little difference within the range of conditions of interest. The coefficients I_o and c could be easily added to restore a reasonable value of cuticular resistance.

The variable TRAN, introduced in equation (5.1) represents transpiration rate in cm^3 water cm^{-2} leaf area and is then calculated using leaf conductance as

$$TRAN = AHDF * GS * LA \qquad (5.22)$$

where

AHDF = the leaf to air absolute humidity difference, g cm^3,

GS = leaf conductance, cm s^{-1},

LA = total leaf area of the young citrus tree, cm^2.

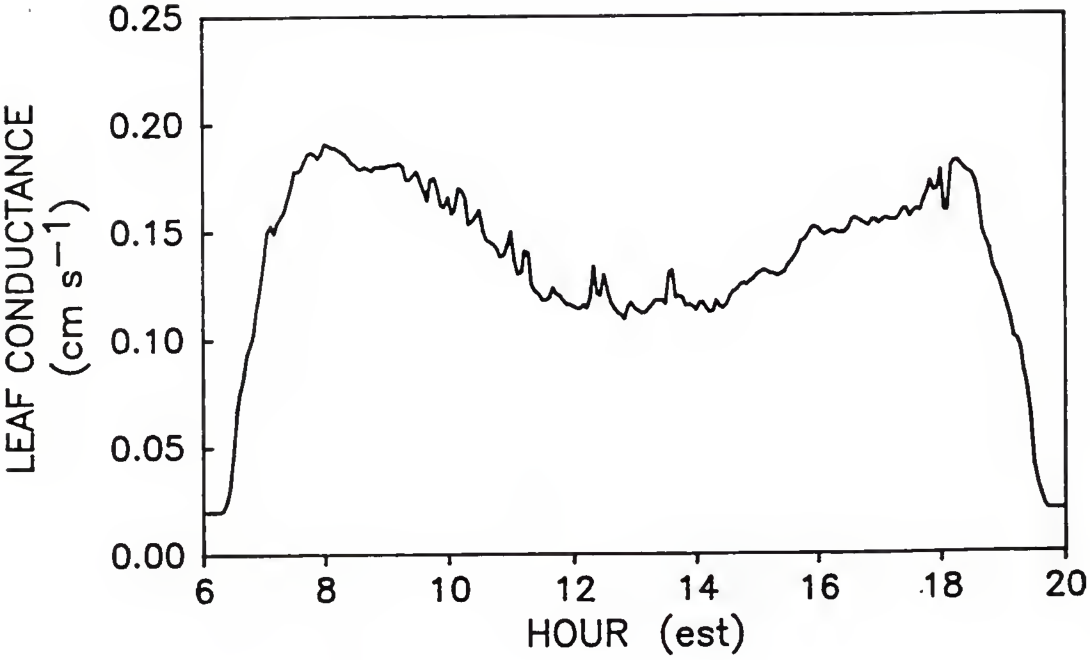


Figure 5.10 Diurnal pattern of leaf conductance calculated with equation (5.20) for fully irrigated citrus trees on Astatula fine sand using weather data from the soil-plant-atmosphere chambers on 30 July 1986.

Sensitivity Analyses of Leaf Conductance Response to Radiation, Humidity and Soil Water Potential

Sensitivity analyses were conducted to describe the manner in which the three environmental variables: photosynthetically active radiation, leaf-to-air humidity deficit, and soil water potential might affect leaf conductance as calculated by equation (5.20). The relationship between leaf conductance over a range of any two environmental variables was predicted while holding the third variable at a low, or nonstressful level.

When nonstressful levels of humidity deficit and soil water potential were specified, the predicted relationship between leaf conductance and radiation increased rapidly between 0 and 400 μmol m^{-2} s^{-1} and at a much reduced rate beyond 400 μmol m^{-2} s^{-1} (Figure 5.11). As the humidity deficit was increased, or soil water potential was reduced, leaf conductance was reduced at all levels of radiation. Leaf conductance was reduced severely as humidity deficit was increased from 0 to 20 g m^{-3} regardless of the level of radiation and at all levels of soil water potential except at -5000 cm water; at this level of soil water potential leaf conductance was very low regardless of the humidity deficit (Figure 5.12). An increase in humidity deficit from 5 to 20 g m^{-3} represents an increase that might easily be incurred diurnally in Florida during the summer. Equation (5.20) predicted that such an increase in humidity deficit would result in leaf conductance being reduced by more than half. Predicted leaf conductance dropped rapidly as soil water potential declined from 0 to -1000 cm water, except when the humidity deficit was greater than 20 g m^{-3} (Figure 5.13). In

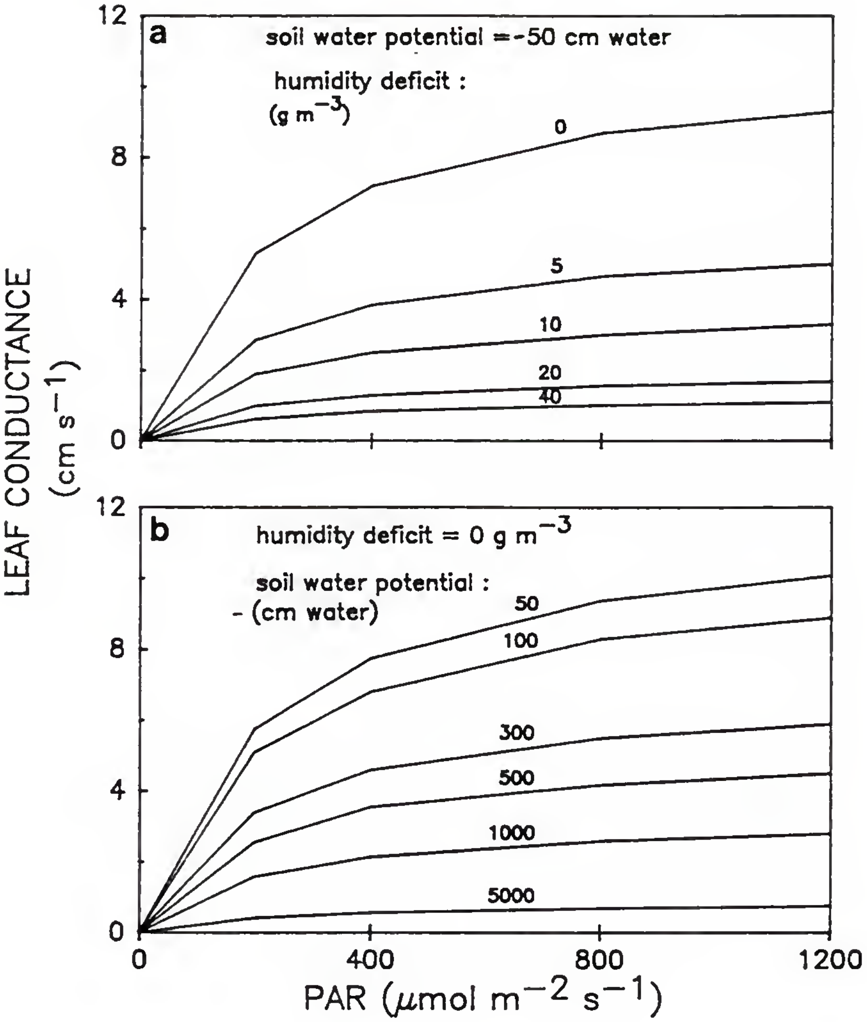


Figure 5.11 Leaf conductance response to photosynthetically active radiation (PAR) at: a) a constant soil water potential of -50 cm water over a range of leaf-to-air humidity deficits and, b) at a constant leaf-to-air humidity deficit over a range of soil water potentials.

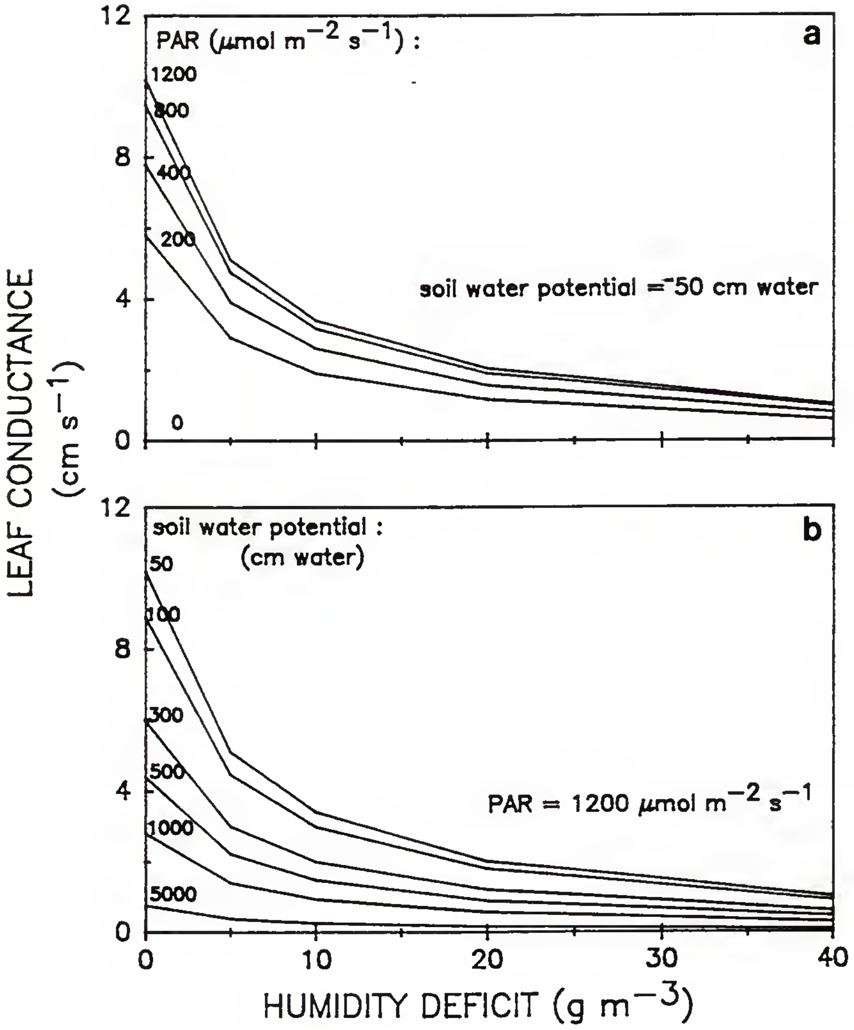


Figure 5.12 Leaf conductance response to leaf-to-air humidity deficit at: a) a constant soil water potential of -50 cm water over a range of photosynthetically active radiation (PAR) and, b) at a constant radiation level of 1200 μmol m^{-2} s^{-1} over a range of soil water potentials.

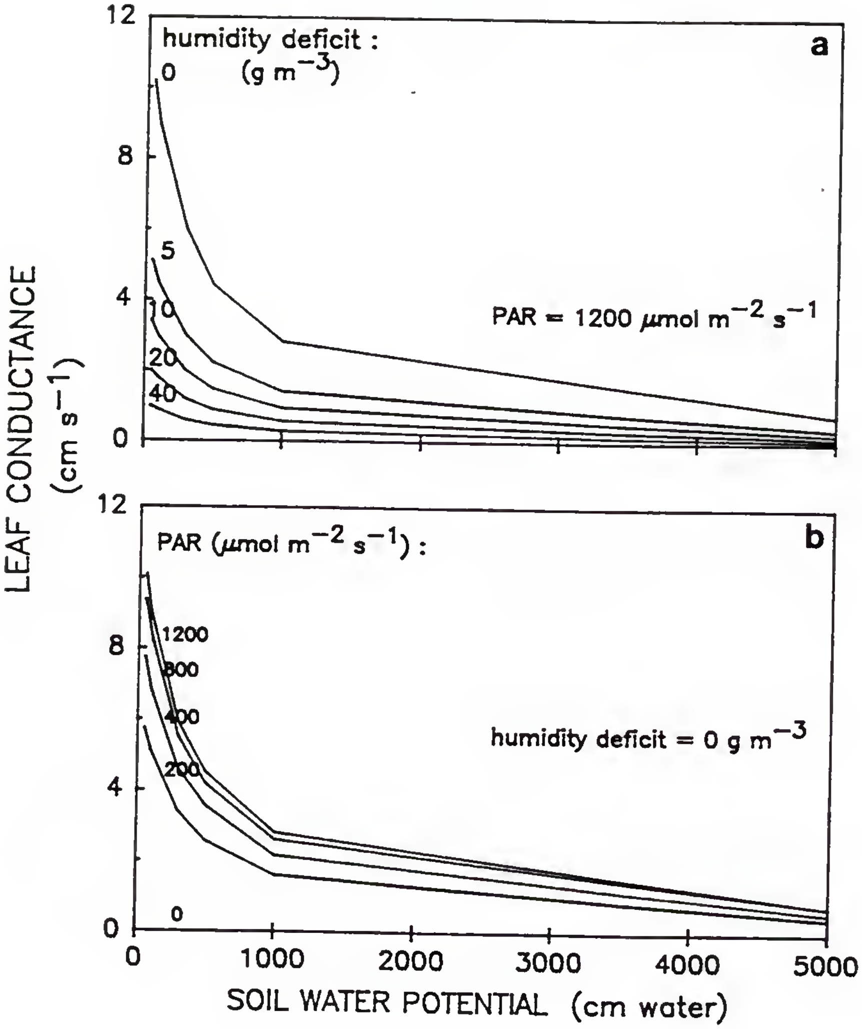


Figure 5.13 Leaf conductance response to soil water potential at: a) a constant photosynthetically active radiation (PAR) level of 1200 µmol m^{-2} s^{-1} over a range of leaf-to-air humidity deficits and, b) at a constant humidity deficit of 0 g m^{-3} over a range of PAR levels.

summary, equation (5.20) predicted that citrus leaf conductance increased rapidly between 0 and 400 μmol m^{-2} s^{-1} photosynthetically active radiation and was reduced severely at leaf-to-air humidity deficits of 20 g m^{-3} or greater or at soil water potentials below -1000 cm water.

Diurnal patterns of leaf conductance were calculated using the photosynthetically active radiation data from the SPAR chamber on 30 July 1986 (Figure 5.3) at a high soil water potential (-10 cm water) over a range of leaf-to-air humidity deficits (Figure 5.14). Most noticeable is the large reduction in leaf conductance as humidity deficit rose from 0 to 5 g m^{-3}. As humidity deficit increased leaf conductance response to radiation was dampened and at 30 g m^{-3} leaf conductance remained less than 0.25 cm s^{-1} throughout the day. Maximum diurnal transpiration decreased from about 13.5 to 3.0 mmol m^{-2} s^{-1} as humidity deficit increased from 0 to 40 g m^{-3}.

At a constant humidity deficit of 5 g m^{-3}, the maximum leaf conductance was reduced by about half, 0.51 to 0.23, as soil water potential decreased from -50 to -500 cm water (Figure 5.15). At a humidity deficit of 40 g m^{-3}, leaf conductance at all levels of water potential was severely reduced as compared to values at the low humidity deficit. Similarly, diurnal maximum transpiration was severely reduced over this range of soil water potentials as the humidity deficit was raised from 5 to 40 g m^{-3} (Figure 5.16).

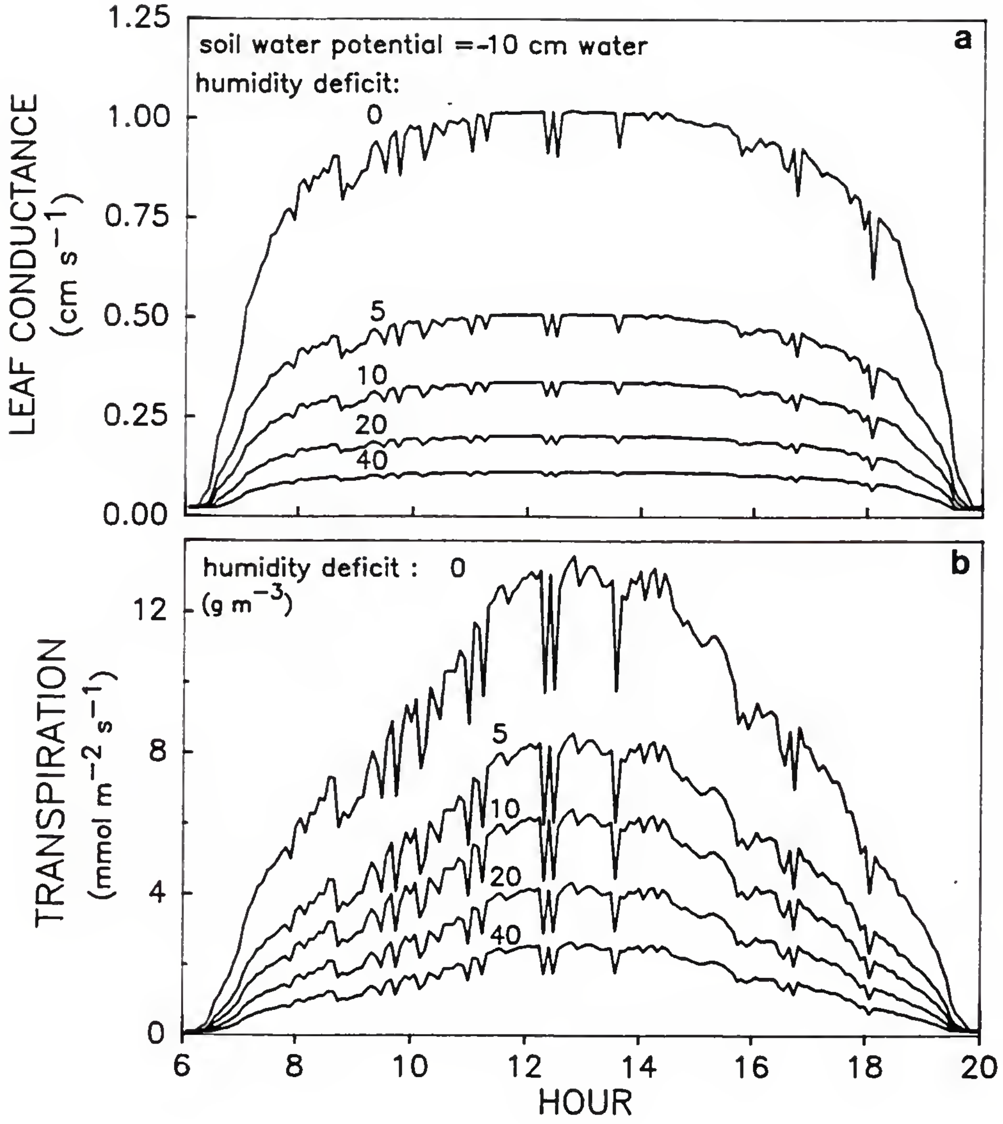


Figure 5.14 Simulated diurnal pattern of citrus leaf conductance and transpiration rates at a constant soil water potential of -10 cm water and over a range of leaf-to-air humidity deficits.

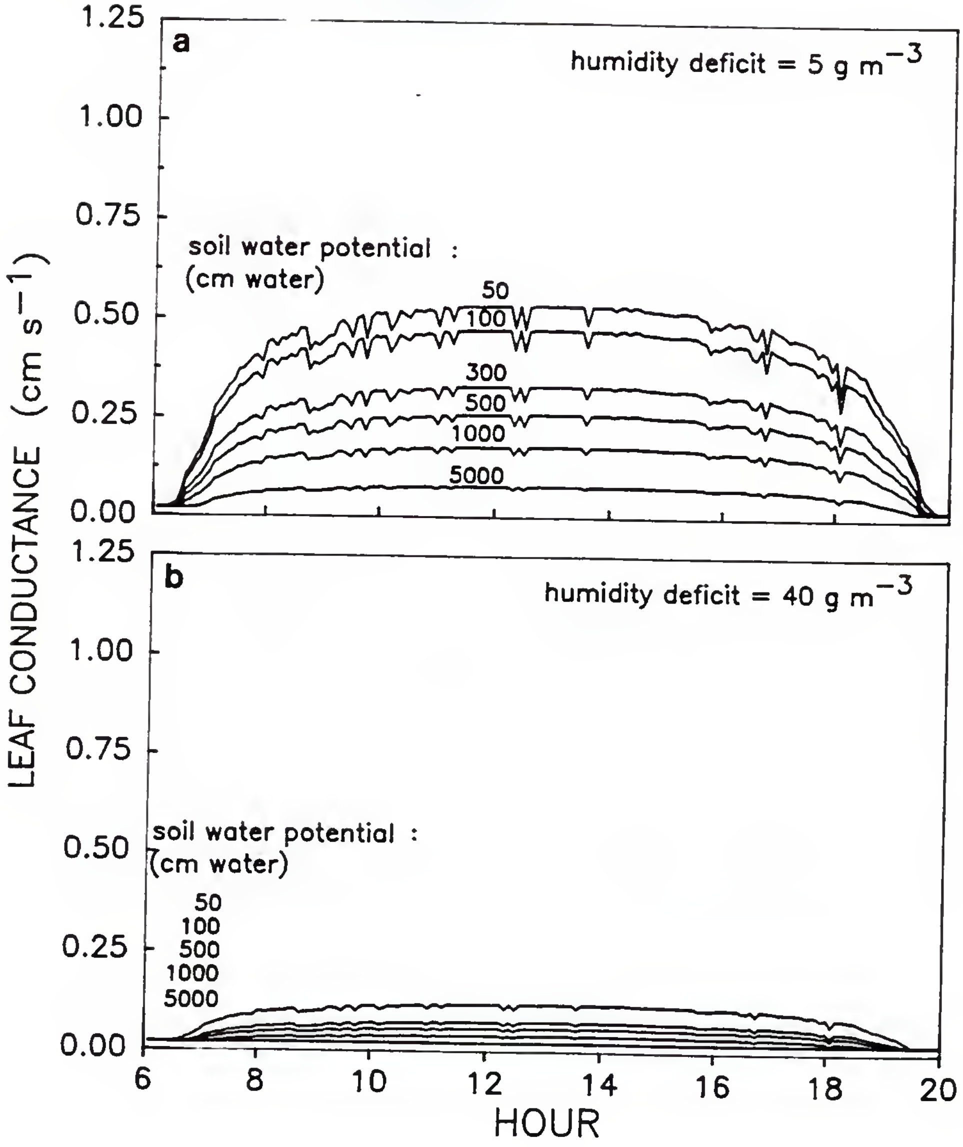


Figure 5.15 Simulated diurnal pattern of citrus leaf conductance at two constant levels of leaf-to-air humidity deficit (5 and 40 g m^{-3}) over a range of soil water potentials.

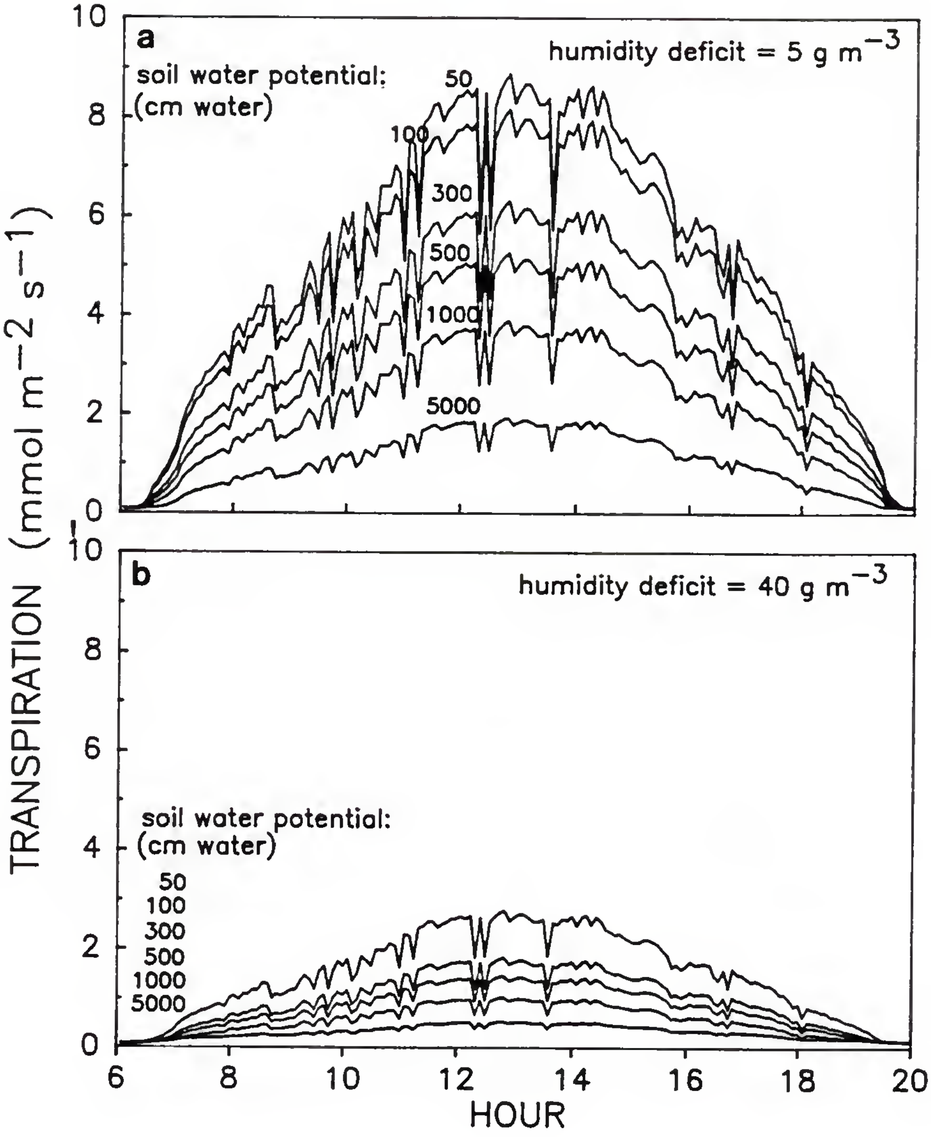


Figure 5.16 Simulated diurnal pattern of citrus transpiration at two constant levels of leaf-to-air humidity deficit (5 and 40 g m^{-3}) over a range of soil water potentials.

Sensitivity analyses were also conducted to investigate alternate ways of calculating WP, the effective soil water potential factor, which is used in equation (5.20) to calculate leaf conductance. Method One calculates WP from the average volumetric water content of the first compartment in the all quadrants and incorporates a plant water storage factor (Method One, described on pages 27 and 28). Thus, using Method One

$$WP = -[\sum_{LY}^{L=1} (\psi_{L,1} + \ldots + \psi_{L,1})/LY] \qquad (5.23)$$

where

L = the soil quadrant,

LY = the total number of soil quadrants.

This method supposes that both irrigated and nonirrigated sections of root have an effect on leaf conductance. Possible mechanisms of these effects may be plant tissue water status effect on stomatal aperature or modification of growth regulator production in roots.

Using Method Two, the effective soil water potential is calculated as

$$WP = -[\sum_{LY_{(irr)}}^{L=1} (\psi_{L,1} + \ldots + \psi_{L(irr),1})/LY_{(irr)}] \qquad (5.24)$$

where $LY_{(irr)}$ is the total number of irrigated soil quadrants.

Method Two calculates WP as the average water potential in the first compartment surrounding the roots in the irrigated portions of soil only and does not include a water storage factor. This method, appropriate to use only when the nonirrigated portions of the soil are at wilting point, reflects the concept that shoot water status and water loss are determined by the water status of the irrigated portions of soil alone. Thus, no deleterious effects on shoot water status are produced by the portion of roots in the dry soil.

Using Method Three, leaf conductance is represents the average leaf conductance calculated using equation (5.20) and the soil water potential of the cylindrical shell compartment closest to the root in each quadrant of soil, i.e., leaf conductance is calculated separately for each quadrant then summed and divided by four

$$Gs = \{ \sum_{LY}^{L=1} [Gs(\psi_{L,1}) + \ldots + Gs(\psi_{LY,1})]\}/LY \tag{5.25}$$

A plant water storage factor is not included. This method reflects the concept that the portion of roots in the nonirrigated quadrants of soil contribute equally, in a negative manner, to shoot water loss.

The three methods of calculating WP were used in simulations of leaf conductance and water use of citrus trees on Parkwood variant fine sandy loam using weather data from 30 July 1986 (Figures 5.17 and 5.18). The behavior of leaf conductance of one-quarter irrigated trees illustrates the greatest differences between the three methods. On day one, maximum leaf conductance was reduced with reduction in the fraction of roots irrigated using methods One and Three. Method Two resulted in equal leaf conductance at all levels of irrigation on the first day.

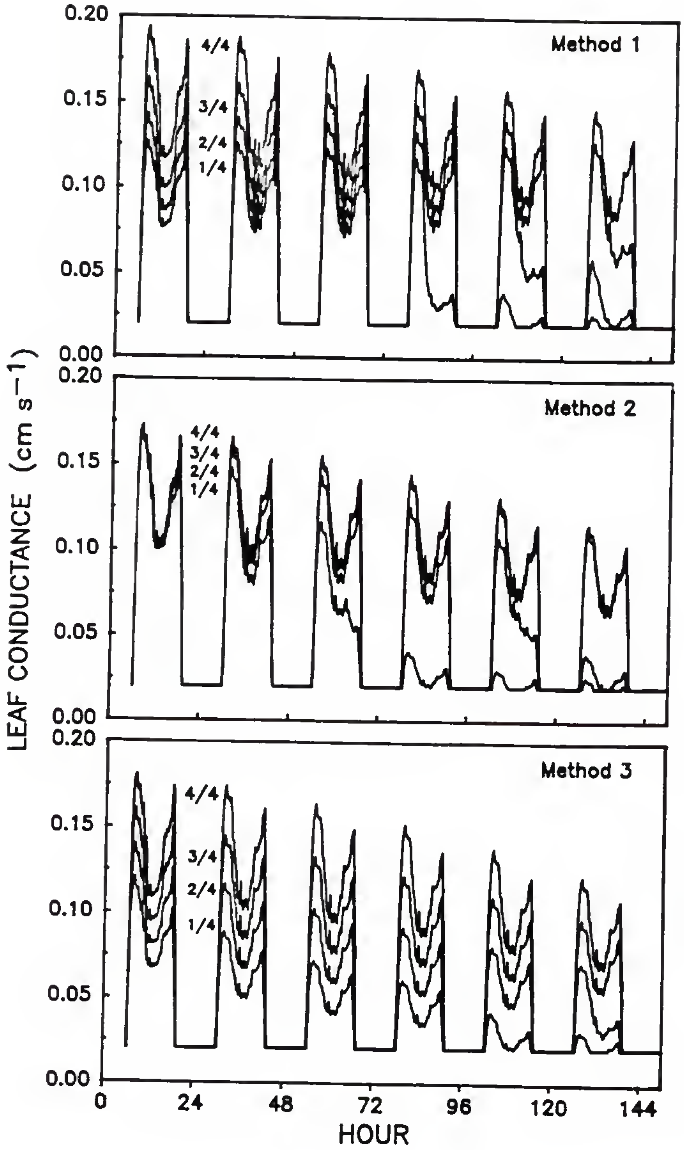


Figure 5.17 Simulated leaf conductance of citrus trees with 4/4, 3/4, 2/4, or 1/4 of their rooting-volume irrigated, using Methods One, Two, and Three of calculating the effective soil water potential.

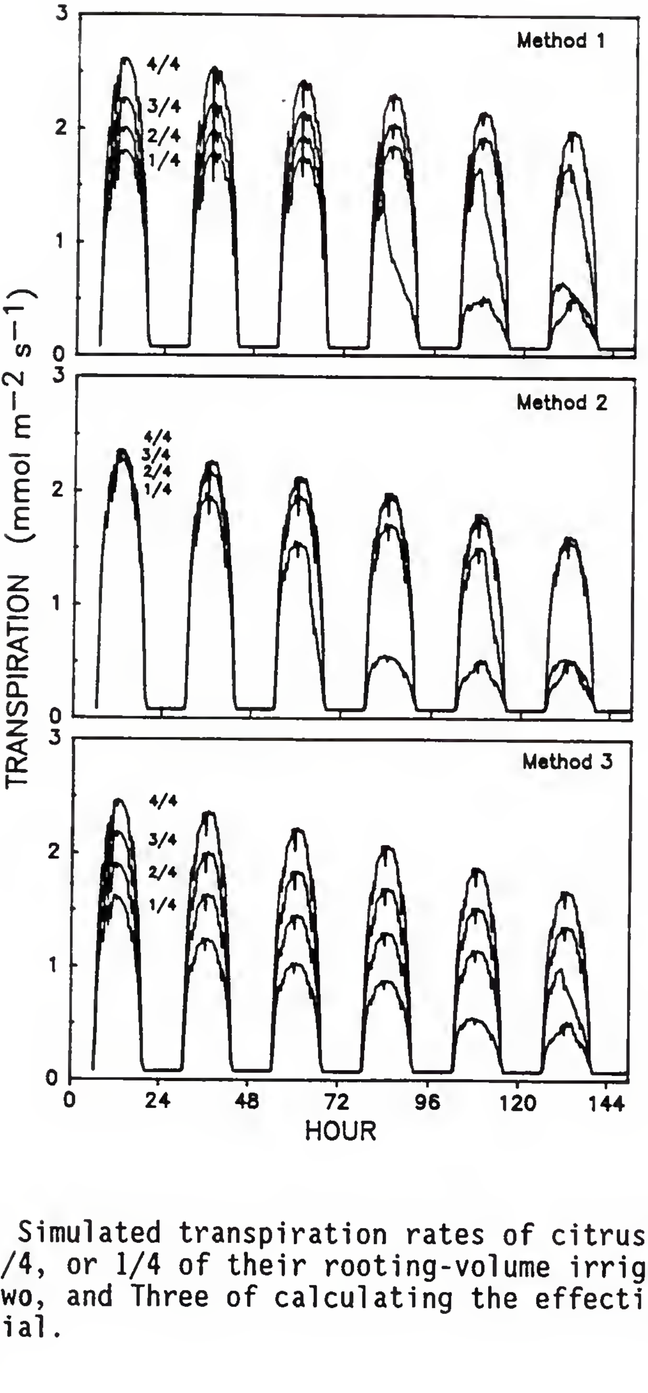


Figure 5.18 Simulated transpiration rates of citrus trees with 4/4, 3/4, 2/4, or 1/4 of their rooting-volume irrigated, using Methods One, Two, and Three of calculating the effective soil water potential.

As soil water was depleted, leaf conductance of the one-quarter irrigated trees decreased only slightly during the first three days using Method One. On the fourth day leaf conductance and transpiration declined rapidly reflecting a rapid drop in soil water potential in the irrigated quadrants. Using Method Two, leaf conductance of the one-quarter irrigated trees began to decline by the middle of the third day and was severely depressed by the fourth day. This method resulted in the highest leaf conductances of one-quarter irrigated trees at the beginning of the simulation and therefore the fastest soil water depletion. Leaf conductance and transpiration of fully and three-quarters irrigated trees remained essentially the same during the six-day period using Method Two. Leaf conductance calculated with Method Three decreased with reduction of irrigated rooting volume in a consistent manner throughout the six-day period. Water use of one-quarter irrigated trees was restricted the most using this method. This resulted in the lowest conductances and transpiration rates of one-quarter irrigated trees. But, by day five leaf conductance and transpiration were almost the same using Method One or Method Three.

Canopy transpiration rates of fully and partially irrigated citrus trees measured in the chambers in 1986 typically showed some separation between treatments, particularily between fully irrigated and the partially irrigated treatments, and therefore behaved more similarily to leaf conductance patterns obtained using Method One or Three at the high soil water content. As soil water content declined, maximum daily transpiration was reduced at each level of irrigation but had a diurnal pattern similar to the diurnal solar radiation pattern. In other words, the shape of the diurnal transpiration curve was more similar to transpiration rates calculated using either Method Two or Three than Method One. Transpiration rates recorded in the SPAR chambers in 1986 at no time showed the precipitous decline that is illustrated by transpiration of the one-quarter irrigated trees calculated using Method One. On the other hand, maximum diurnal transpiration rate of citrus trees did not exhibit a nearly constant rate of reduction with progressive soil water depletion as was indicated using Method Three.

Results

Model Validation

Simulated and actual transpiration rates of fully irrigated citrus trees

To determine whether predicted water use rates from the model reasonably approximated actual rates, evapotranspiration data collected from fully irrigated citrus trees in the SPAR chambers in 1986 were compared to simulated transpiration rates of a single citrus tree. These data were collected at 300-second intervals from cooling coil condensate measured by tipping-bucket rain gauges. Evapotranspiration data collected in the chambers were calculated per m^2 ground area and were expressed on an equivalent leaf area index basis to facilitate comparison with simulated transpiration rates. Actual and simulated water use rates of fully irrigated citrus trees using radiation and temperature data for 30 July 1986 are shown in Figure 5.19 and using data from 28 August 1986 in Figure 5.20.

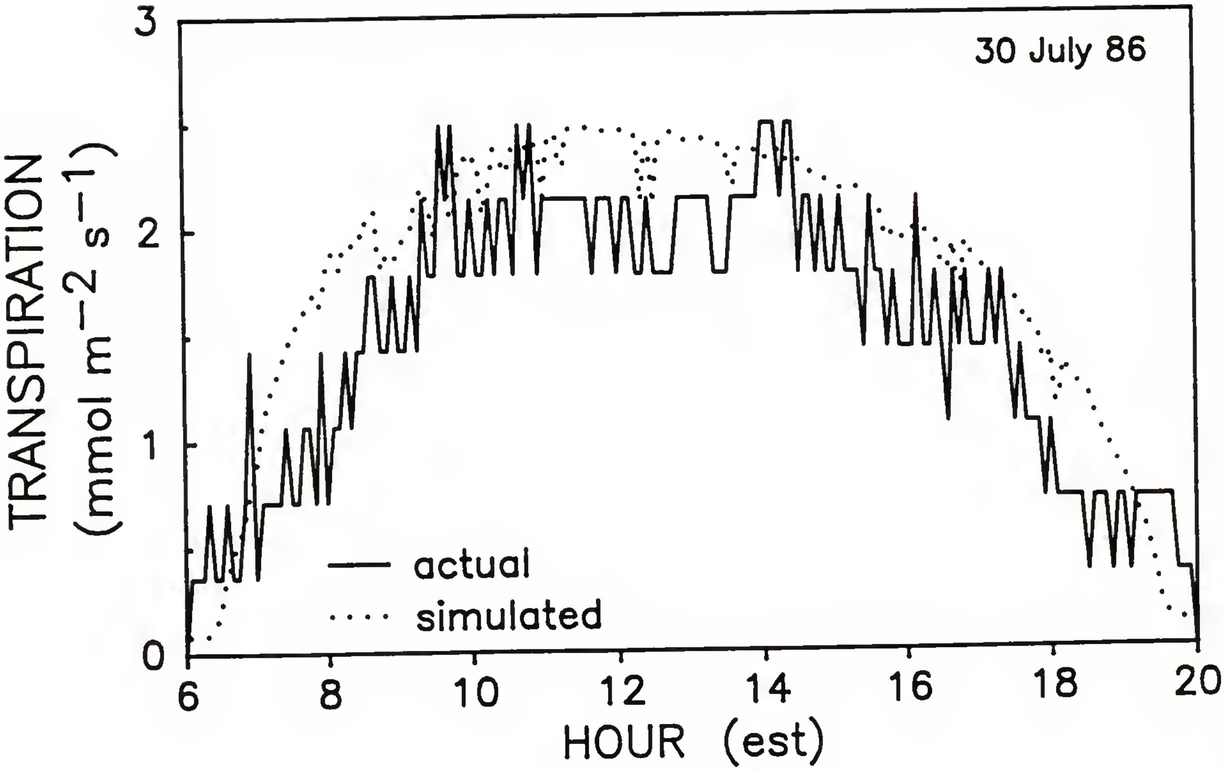


Figure 5.19 Diurnal evapotranspiration rates of fully irrigated citrus trees recorded in the soil-plant-atmosphere chambers on 30 July 1986 and simulated transpiration rates for citrus on builders' sand using weather data from the same day.

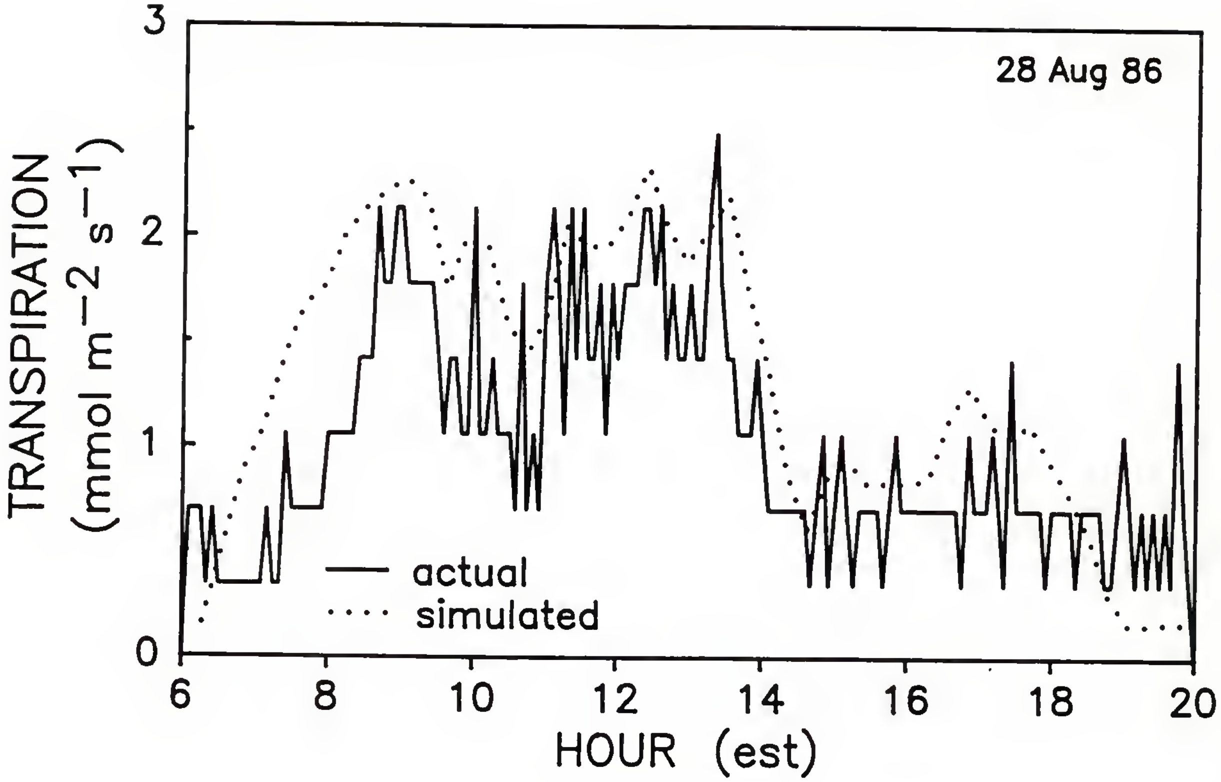


Figure 5.20. Diurnal transpiration rates of fully irrigated citrus trees recorded in the soil-plant-atmosphere chambers on 28 August 1986 and simulated transpiration rates of citrus trees on builders' sand using weather data from the same day.

On both days, simulated transpiration rates after 0700 EST rose steadily, above actual rates, and may reflect greater sensitivity of leaf conductance to radiation than to humidity difference predicted by the model than actually occurred. Simulated transpiration rates were slightly higher than recorded rates throughout most of the day and may be due, in part, to the assumption that all leaves received equal irradiance and were transpiring at the potential rate. This assumption was based on the low leaf area index of young citrus trees in the field. The actual net radiation load on leaves will be attenuated through the canopy as a function of the leaf area index and may be roughly approximated by the equation

$$I = I_o e^{-f(LAI)} \tag{5.26}$$

where

I = net radiation intercepted by the leaf,

I_o = net radiation above the canopy,

f = a crop coefficient that depends on crop species and canopy geometry.

Use of this expression when calculating the actual radiation intercepted by leaves of the citrus tree may improve estimates of water use.

Another significant difference between the actual and simulated data is the apparent inability of the model to simulate the rapid, large increases and decreases in transpiration rates that were observed in the chambers and coincided with periods of decreased and increased radiation, respectively. Observed responses suggest a tighter coupling between leaf conductance and atmospheric humidity deficit than the model was able to predict or may simply reflect the larger time intervals over which the tipping-bucket rain gauges measure transpiration compared to the time steps used in simulations. Also, early morning (before 0700 EST) and late afternoon (after 1900 EST) simulated water-use rates were lower than observed rates. Again, this difference may indicate that actual transpiration rates increased rapidly in response to rising dry-bulb temperature and vapor pressure deficits whereas simulated transpiration rates remained low responding primarily to low radiation levels. Several other possibilities for this behavior may be that leaf conductance at near zero light may be too low due to I_o being eliminated in equation (5.9) and hence causing cuticular resistance to approach infinity, or that evaporation from the soil surface or vat floor in the SPAR chambers constituted a large part of evapotranspiration on this day. Overall, the model predicted the rates and diurnal patterns of transpiration by fully irrigated citrus trees on the selected dates within a reasonable range.

Simulated and actual transpiration rates of partially irrigated trees

Simulated transpiration rates of fully and partially irrigated citrus trees using weather data and available soil water levels from the SPAR chambers on 1 August and 4 July 1986 are compared in Figures 5.21 and 5.22, respectively. Simulated transpiration rates, at all levels of irrigation, were higher during the middle of the day than actual rates. Whereas transpiration of one-half and one-quarter irrigated trees in the chambers remained quite constant throughout the middle of the day, simulated transpiration rates increased to a peak at mid-day and dropped

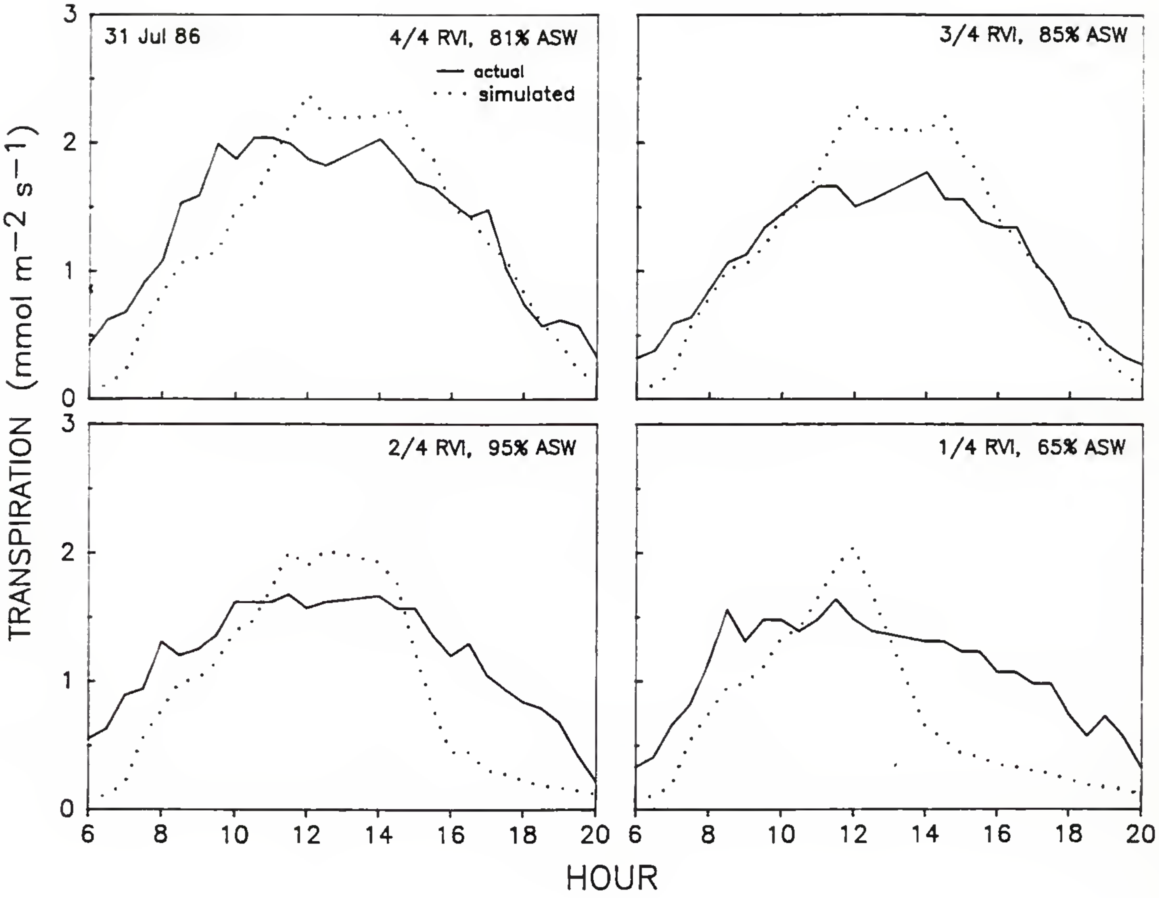


Figure 5.21 Actual and simulated transpiration rates of fully and partially irrigated citrus trees using available soil water (ASW) levels and weather data from 31 July 1986.

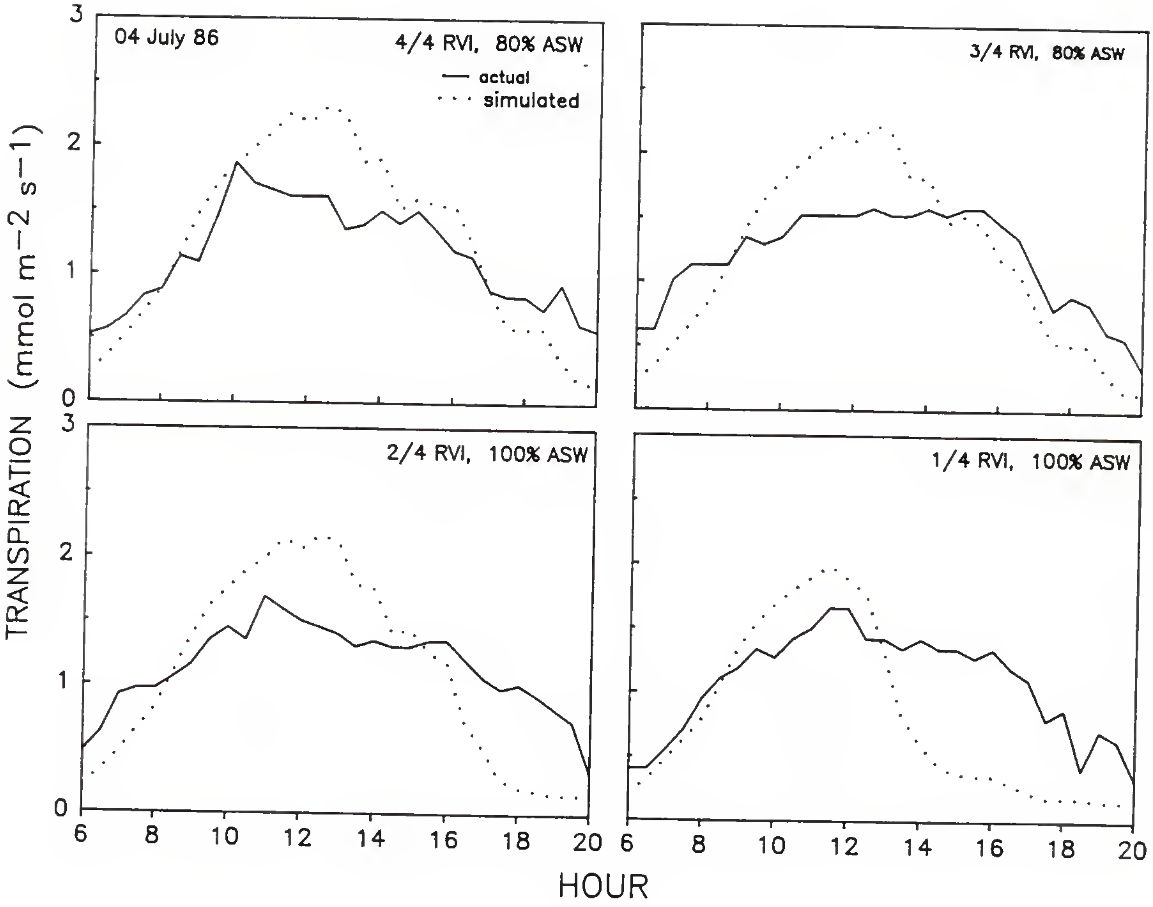


Figure 5.22 Actual and simulated transpiration rates of fully and partially irrigated citrus trees using available soil water (ASW) levels and weather data from 4 July 1986.

off steadily during the remainder of the day. It appears that citrus trees in the chambers had reduced leaf conductances during the middle of the day, perhaps closing to a greater extent in response to high humidity deficits than did simulated leaf conductances.

Simulated transpiration rates dropped off more rapidly in the one-half or one-quarter irrigated trees than was actually observed in the chambers. There are several possibilities for this behavior: 1) the predicted water use of trees at these levels of irrigation resulted in more rapid depletion of soil water and thus earlier reduction of leaf conductance, 2) water flow in the soil to the roots is underestimated thus the model overpredicts water depletion in the vicinity of the roots at these levels of irrigation, 3) other factors not accounted for in the model permitted greater supply of water to roots, 4) leaf conductance of trees in the chambers did not respond to soil water potential in the manner described in the model, 5) a 0.6-cm perched water table in the compartments may have supplied some water by capillarity in the afternoon. These results indicate that the model predicts transpiration rates of fully and three-quarters rooting-volume irrigated trees reasonably well, but overestimates the reduction in transpiration of the one-half, and particularly, the one-quarter, irrigated citrus trees.

Simulated Response of Citrus Trees to Soil Water Depletion

When simulated water potentials in the cylindrical shell soil compartment adjacent to the roots dropped below 330 cm water, bars leaf conductance and transpiration rate dropped rapidly, regardless of the number of quadrants irrigated. This response occurred earliest in the simulation for trees with only one-quarter of their root system irrigated and was delayed as the fraction of root volume irrigated was increased. This behavior is illustrated in graphs of leaf conductance for citrus trees on Parkwood variant fine sandy loam (Figure 5.23). On day one of the simulation, maximum leaf conductance was reduced by 11, 23, and 31% in trees with 3/4, 2/4, and 1/4 of their rooting volume irrigated, respectively, as compared to fully irrigated trees. Simulated leaf conductance fell precipitously, first in plants with only one-quarter of their rooting volume irrigated. Severe reduction was delayed by about one day from that time with each incremental increase in the rooting volume irrigated. On the coarse-grained Astatula fine sand, maximum leaf conductance was reduced by only 3, 5, and 8% compared to values recorded for fully irrigated trees, when 3/4, 2/4, and 1/4 of the rooting volume was irrigated, respectively (Figure 5.24). Severe reduction in leaf conductance occurred earlier on the Astatula fine sand than on the Parkwood fine sandy loam; by the middle of the third day of the simulation leaf conductance was severely reduced in trees with only one-quarter of their rooting volume irrigated on the Astatula fine sand compared to the middle of the fourth day for trees on the Parkwood sandy loam.

On both soils, the relationship between the reduction in predicted transpiration and reduction in irrigated rooting volume was not proportional, i.e., a 50% reduction in irrigated rooting volume did not result in a 50% reduction in transpiration (Figures 5.25, 5.26). On day six on the Parkwood soil, transpiration of the three-quarters irrigated

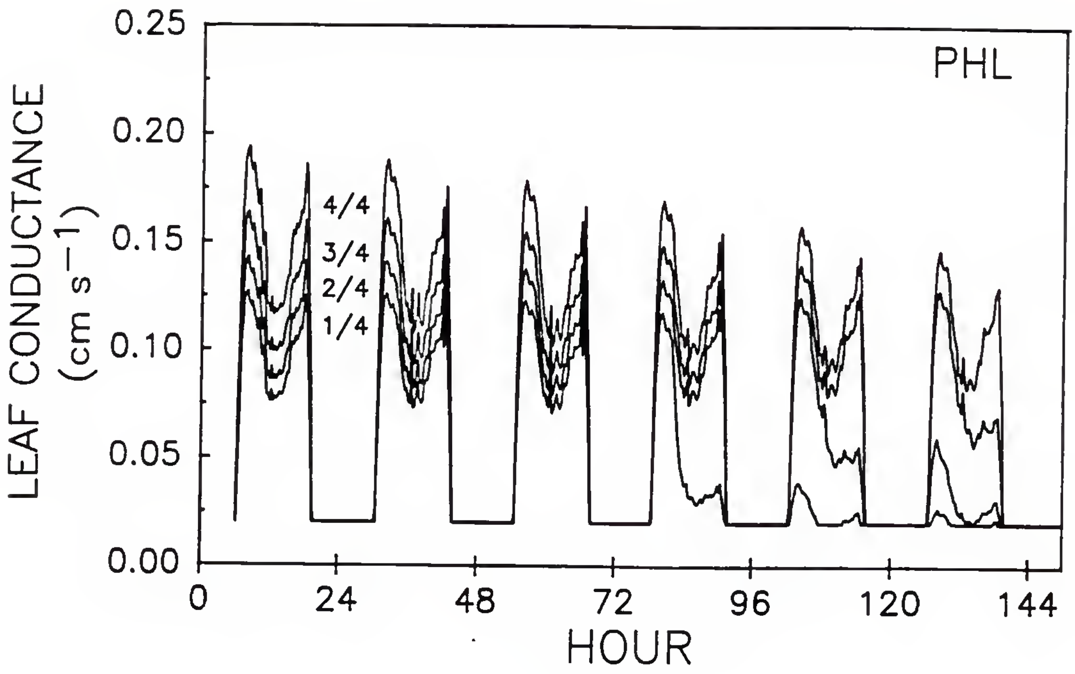


Figure 5.23 Simulated leaf conductance of citrus trees on Parkwood variant fine sandy loam (P) at the high dry-bulb temperature (H) and low root length density (L), with 4/4, 3/4, 2/4 or 1/4 of the rooting volume irrigated.

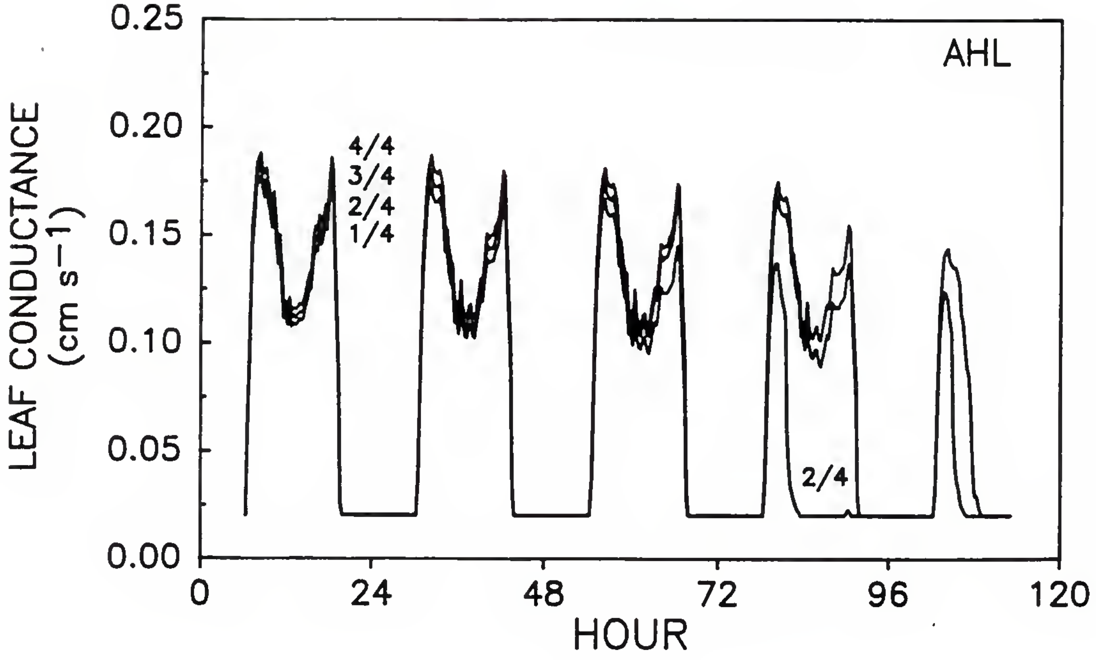


Figure 5.24 Simulated leaf conductance of citrus trees on Astatula fine sand (A) at the high dry-bulb temperature (H) and low root length density (L), with 4/4, 3/4, 2/4 or 1/4 of the rooting volume irrigated.

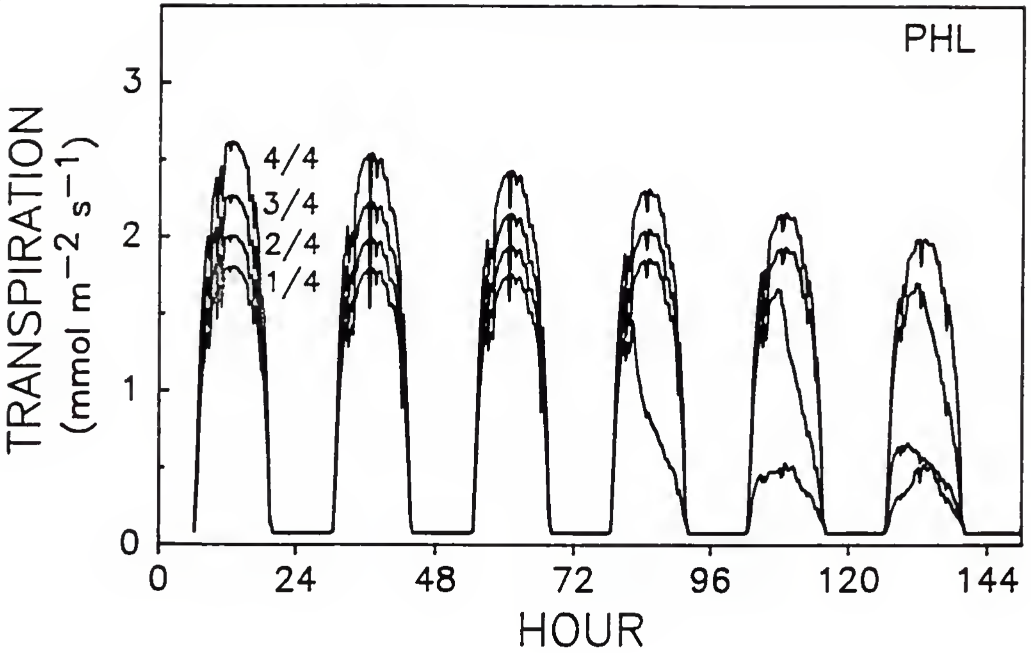


Figure 5.25 Simulated transpiration rates of citrus trees on Parkwood variant fine sandy loam soil (P) at the high dry-bulb temperature (H) and low root length density (L), with 4/4, 3/4, 2/4 or 1/4 of the rooting volume irrigated.

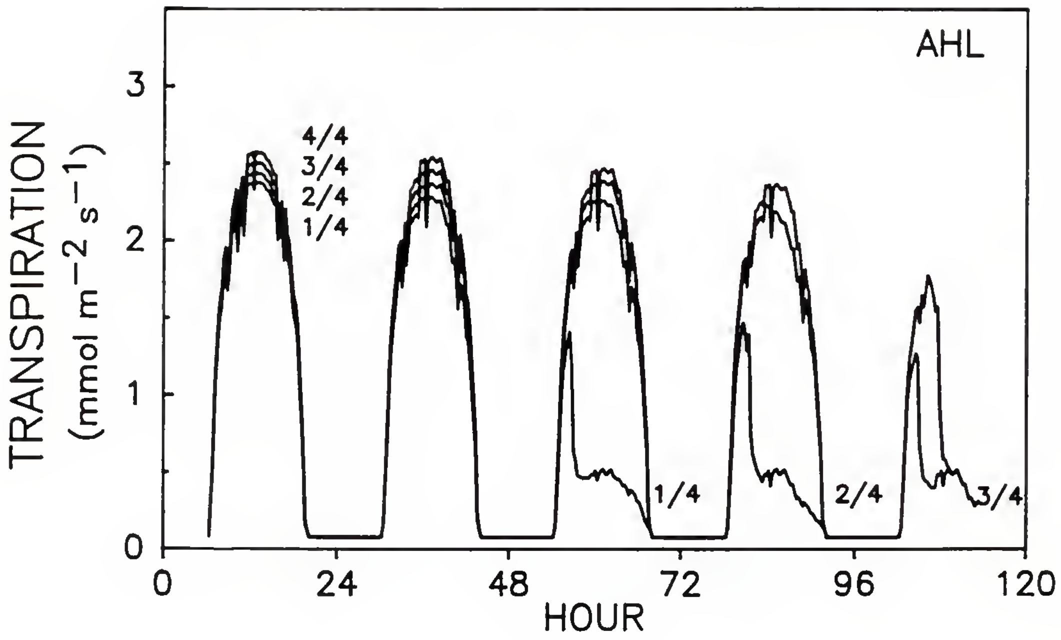


Figure 5.26 Simulated transpiration rates of citrus trees on Astatula fine sand soil (A) at the high dry-bulb temperature (H) and low root length density (L), with 4/4, 3/4, 2/4 or 1/4 of the rooting volume irrigated.

Table 5.1 Reduction in daily maximum transpiration (TR) of fully and partially root volume irrigated (RVI) citrus trees on Parkwood and Astatula soils.

RVI	Tr (mmol m^{-2} s^{-1})	Reduction (%)	Tr (mmol m^{-2} s^{-1})	Reduction (%)
	Parkwood variant fine sandy loam			
	Day 1		Day 6	
4/4	2.61	-	1.98	-
3/4	2.26	13	1.70	14
2/4	2.01	23	0.66	67
1/4	1.80	31	0.53	74
	Astatula fine sand			
	Day 1		Day 3	
4/4	2.58	-	2.38	-
3/4	2.51	3	2.22	6
2/4	2.44	5	1.47	38
1/4	2.38	8	- †	-

tree was reduced by only 14% compared to fully irrigated trees and indicates only a small reduction in the rate of water use compared to water use rates of fully irrigated trees (Table 5.1). In the one-half irrigated trees, transpiration fell by 67% and indicates that the system was unable to maintain the high rates of water transport required. On day six in the one-quarter irrigated trees transpiration was severely reduced, by 74% that of fully irrigated trees. On Astatula fine sand, maximum transpiration on day three of the simulation of trees with three-quarters of their root system irrigated was reduced by only a small amount, 4% compared to that of fully irrigated trees. Transpiration of trees with one-half of their root volume irrigated was reduced by 38%. Plants with one-quarter of their root system irrigated had already depleted water in the vicinity of roots by the third day of the simulation.

Influence of Soil Type on Water Use Rates of Partially Irrigated Citrus

Reductions in leaf conductance and transpiration occurred earlier at all levels of rooting-volume irrigation on the Astatula fine sand than on the Parkwood fine sandy loam and reflect differences in the water holding capacity and capillary conductivity of the two soils. Although a small amount of water was absorbed by roots in nonirrigated portions of soil, most water for transpiration was extracted by roots in the irrigated soil. As the portion of irrigated soil was reduced, greater flux rates in the irrigated soil volume were required in order to maintain transpiration rates. As water was withdrawn from the cylindrical shell soil compartment closest to the roots, it was replaced by water flowing in from the outer cylindrical shell compartments. As soil water was depleted, the effective soil hydraulic conductivity between the cylindrical shell compartments decreased simultaneously so that replacement of water extracted from the first compartment did not occur as rapidly, thus leading to water depletion in the vicinity of roots.

Soil hydraulic conductivity

The relationship between hydraulic conductivity and soil water potential (or volumetric water content) is highly nonlinear and largely dependent on soil texture. Capillary movement of water on the Astatula fine sand at high water contents was greater than on the Parkwood variant fine sandy loam, but as soil water content was reduced, capillary movement of water on the Astatula fine sand was reduced to a greater extent than on the Parkwood fine sandy loam (Figure 5.27). For example, on the Parkwood fine sandy loam hydraulic conductivity did not approach zero until the beginning of the fourth day for one-quarter irrigated trees and was relatively high by the middle of the fifth day for fully irrigated trees (Figure 5.28). On the Astatula soil under the same conditions, soil hydraulic conductivity was reduced essentially to zero by the middle of the second day for one-quarter irrigated trees and by the beginning of the fourth day for fully irrigated trees (Figure 5.29).

Soil water depletion in the vicinity of roots

As the effective hydraulic conductivity of the first compartment was reduced during the simulation, soil water movement to the roots was restricted and resulted in the development of large gradients of water

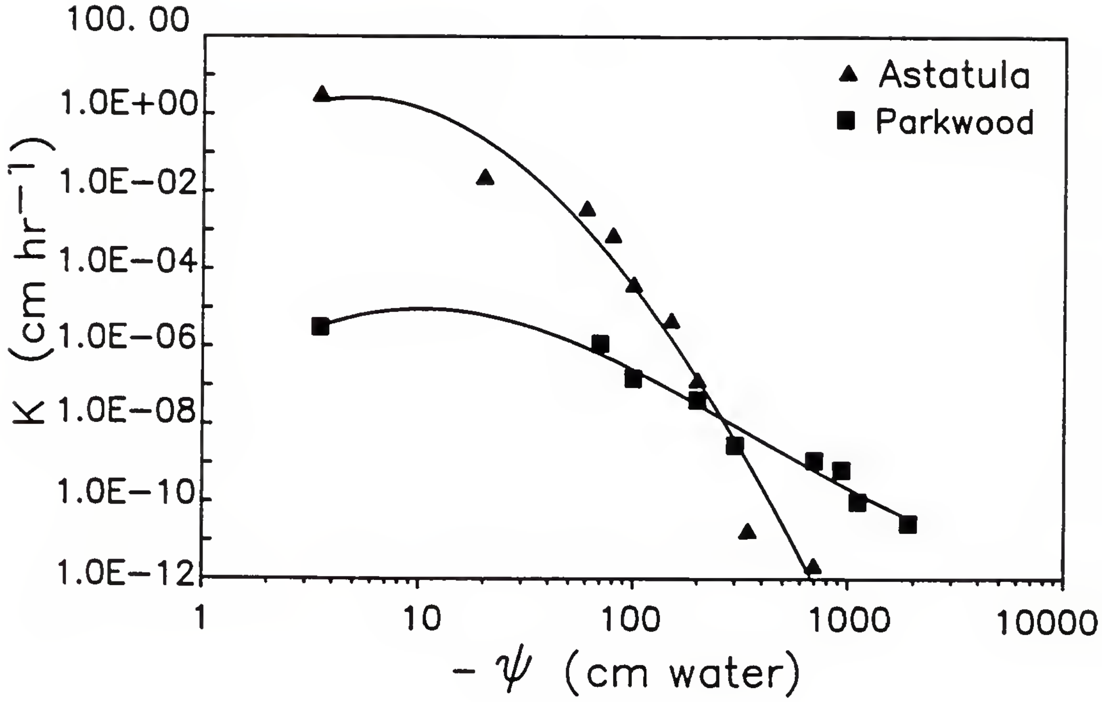


Figure 5.27 Hydraulic conductivities (K) of Parkwood variant fine sandy loam and Astatula fine sand in relation to soil water potential.

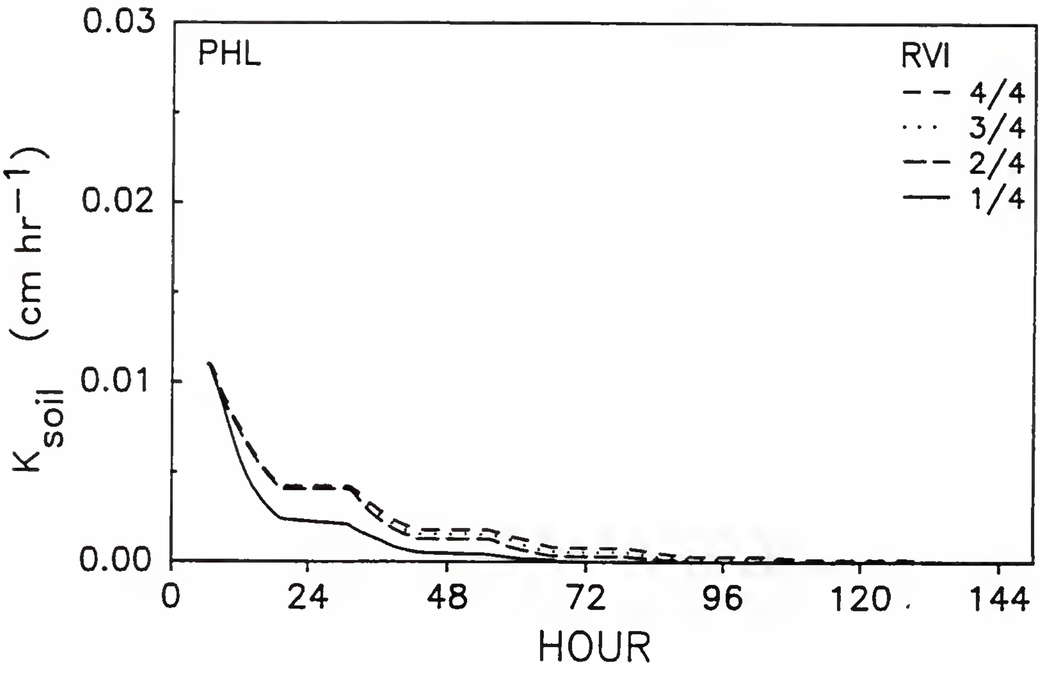


Figure 5.28 Simulated hydraulic conductivity of Parkwood sandy loam (P) with citrus trees at the high-dry bulb temperature (H) and low root length density (L) with 4/4, 3/4, 2/4, or 1/4 of the rooting volume irrigated.

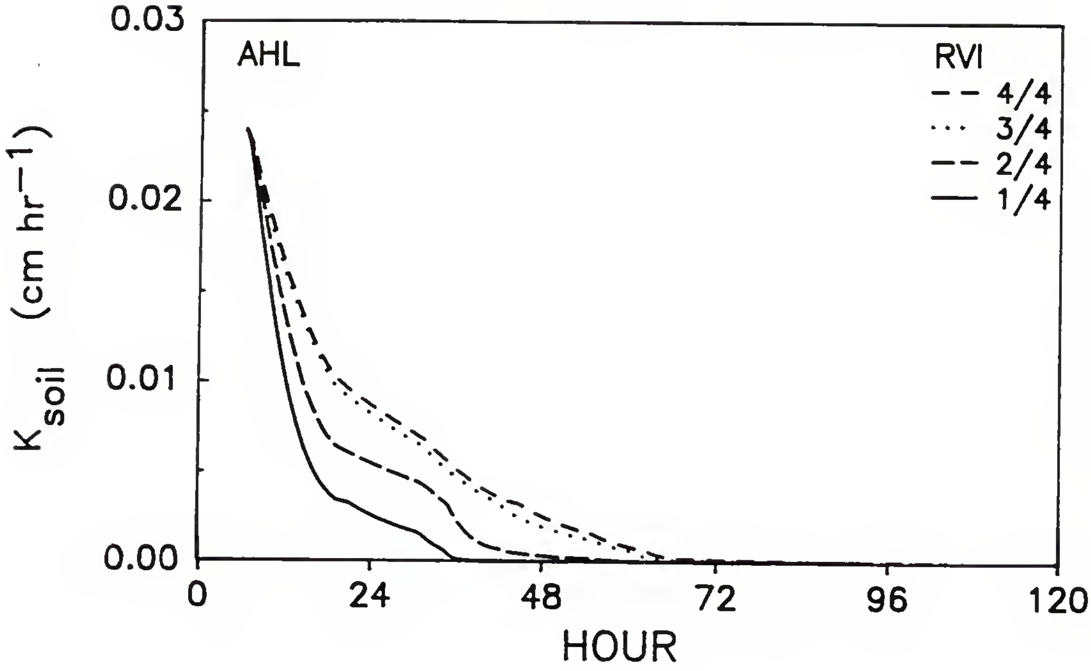


Figure 5.29 Simulated hydraulic conductivity of Astatula fine sand (A) with citrus trees at the low-dry bulb temperature (L) and high root length density (H) with 4/4, 3/4, 2/4 or 1/4 of the rooting volume irrigated.

content and soil water potential with distance from the roots. This behavior can be seen in graphs of changes in water potentials of the concentric soil compartments around the roots. For example, in Figure 5.30 simulated water potentials on the Parkwood soil are shown in compartments 1, 2, 3, and 4, where soil compartment 1 is adjacent to the root and 4 is the outermost compartment. It can be seen that for fully irrigated plants (4/4) water potential gradients in vicinity of the roots at the end of the sixth day were small relative to water potentials that developed in plants with less than their entire rooting volume irrigated. As the fraction of roots irrigated was reduced, water potential gradients developed earlier and were greater in magnitude. By the end of the sixth day, the water potential difference between the innermost and outermost compartments in the one-quarter irrigated treatment was nearly five bars. Water in the vicinity of roots redistributed in the early part of the evening but did not equilibrate throughout all the compartments around the roots. On the Astatula fine sand (Figure 5.31), the most outstanding feature is the precipitous decline in water potential in the compartment adjacent to the roots when water potential reached 0.33 bar. Beyond this point there was no recovery of water potential in this compartment. Water potentials continued to decline gradually in compartments 2, 3, and 4.

As the water content was depleted reduced soil water potentials in the first cylindrical shell soil compartment caused reduced leaf conductance and transpiration. On the Astatula fine sand, maximum transpiration on day one was 2.56 mmol m^{-2} s^{-1} and was reduced to 2.0 mmol m^{-2} s^{-1} after five days. Maximum transpiration on day one on the Parkwood

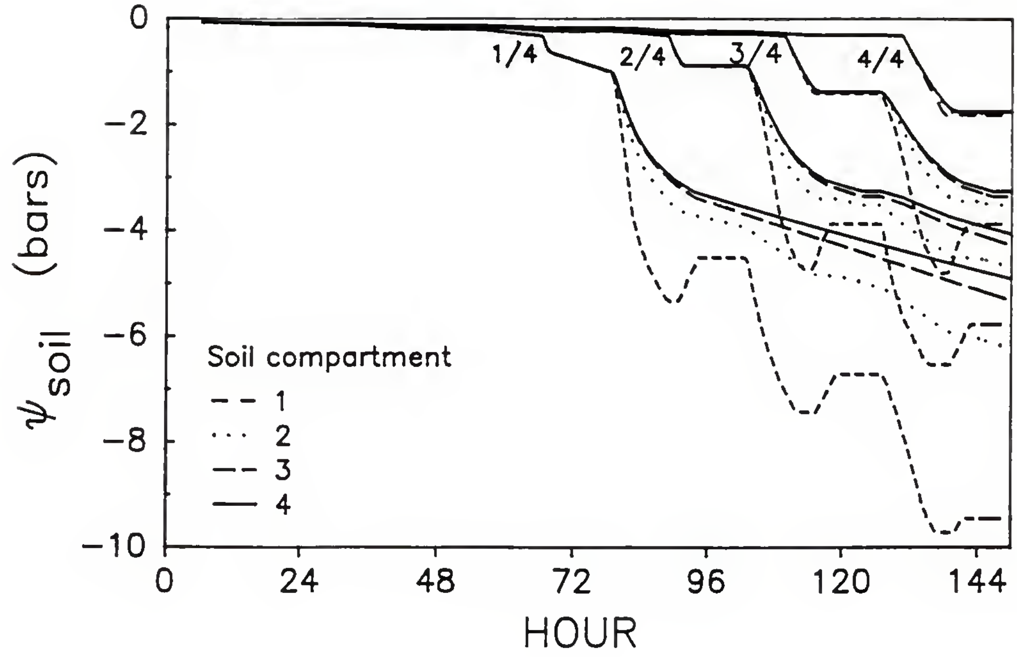


Figure 5.30 Simulated soil water potentials in the cylindrical compartments surrounding the roots of citrus trees on Parkwood variant fine sandy loam (P) at the high dry-bulb temperature (H) and low root length density (L), with 4/4, 3/4, 2/4 or 1/4 of the rooting volume irrigated.

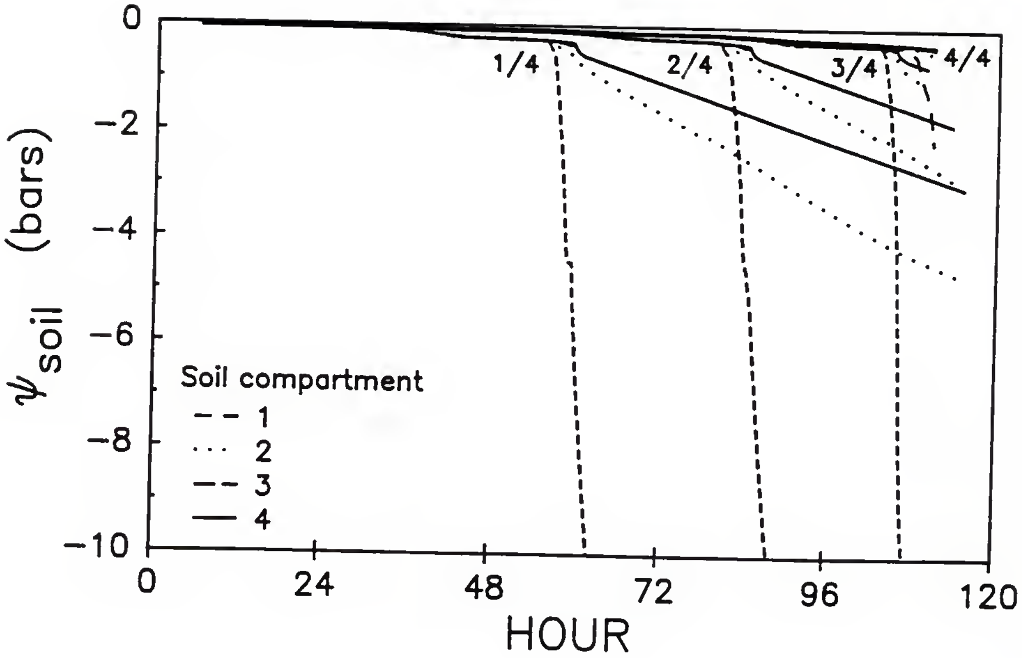


Figure 5.31 Simulated soil water potentials in the cylindrical compartments surrounding the roots of citrus trees on Astatula fine sand (A) at the high dry-bulb temperature (H) and low root length density (L), with 4/4, 3/4, 2/4 or 1/4 of the rooting volume irrigated.

sandy loam was 2.56 mmol m^{-2} s^{-1} and was reduced to 2.10 mmol m^{-2} s^{-1} after six days. The effect was similar at all other levels of irrigation, i.e., severe reduction of transpiration was delayed by one to two days on the Parkwood fine sandy loam compared to reductions on the Astatula fine sand. Thus, for plants on the heavier soil, simulated water extraction at potential rates could proceed for a longer time before the hydraulic conductivity of the soil was reduced to a point where steep gradients of water content in the vicinity of roots developed and prevented redistribution of water to roots and thus closure of stomata.

Water Use of Citrus Trees as Influenced by Root-Length Density

Similar to the effect of reducing the portion of rooting volume irrigated, reduction of the root length density resulted in a reduced root length available for water extraction and thus in increased flux rates in the soil. Increasing root length density from 0.12 to 1.0 cm cm^{-3} permitted slightly greater water use by the plants by reducing water potential gradients in the vicinity of the roots (Figure 5.32). Reduction of simulated transpiration rates was delayed by about one-half day in plants with a root length density of 1.0 cm cm^{-3} compared to plants with a root length density of 0.12 cm cm^{-3}. The effect was greatest for plants with only one-quarter of their rooting-volume irrigated and was more noticeable for plants on the Astatula fine sand then on the Parkwood sandy loam (Figures 5.33 and 5.34).

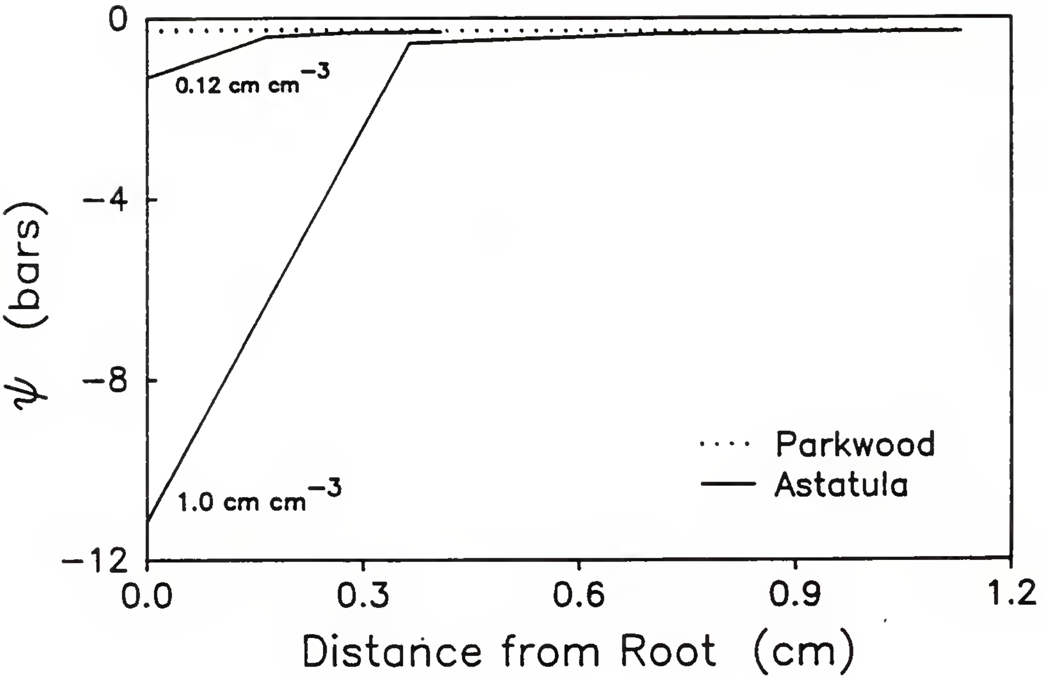


Figure 5.32 Simulated soil water potential gradients around citrus roots on Parkwood variant fine sandy loam and Astatula fine sand at two levels of root-length density.

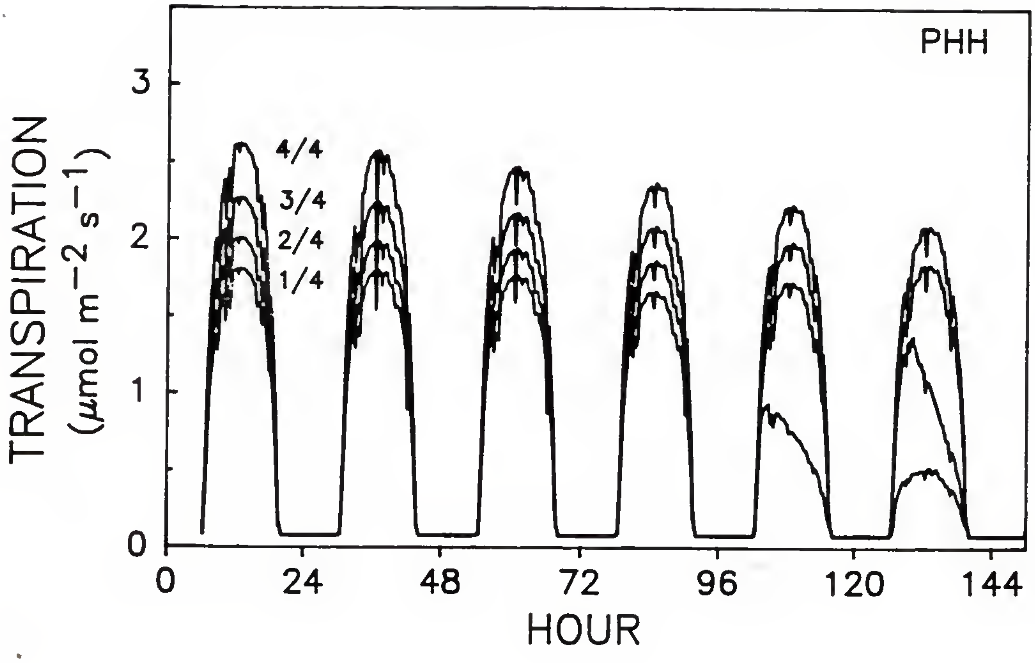


Figure 5.33 Simulated transpiration rates of citrus trees on Parkwood fine sandy loam (P) at the high dry-bulb temperature (H) and high root length density (H), with 4/4, 3/4, 2/4 or 1/4 of the rooting volume irrigated.

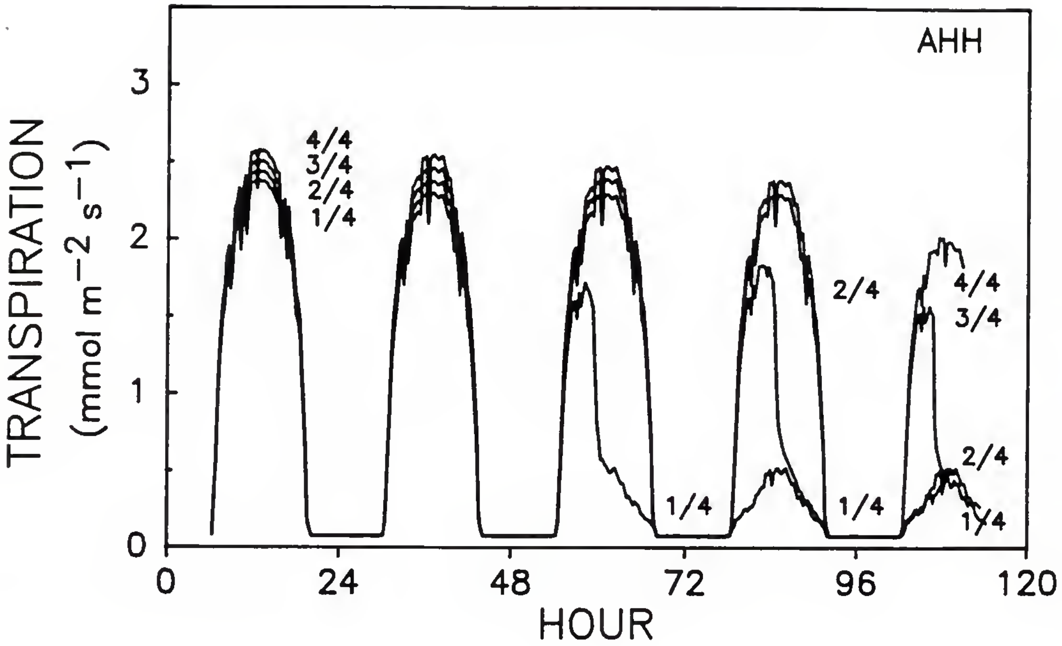


Figure 5.34 Simulated transpiration rates of citrus trees on Astatula fine sand (A) at the high dry-bulb temperature (H) and high root length density (H), with 4/4, 3/4, 2/4 or 1/4 of the rooting volume irrigated.

Influence of Evaporative Demand on Water Use of Citrus Trees

On 30 July photosynthetically active radiation levels reached a maximum of 1700 μmol m^{-2} s^{-1} between 1100 and 1300 EST with only intermittent periods of cloudiness (Figure 5.3). During this period dry-bulb temperature reached 37 °C and maximum atmospheric vapor pressure deficit was 4.2 kPa. The simulated leaf-to-air absolute humidity deficit under these conditions for citrus at a high water content was greater than 41 g m^{-3} between 1100 and 1300 EST and reflects the high dry-bulb temperature as well as high leaf temperature (Figure 5.35). Leaf conductance was reduced severely during this period of high leaf-to-air humidity deficits. The effect of the lower dry-bulb temperature was to reduce leaf-to-air absolute humidity deficit during the day compared to treatments with high dry-bulb temperature. Until about 1400 EST on 28 August solar radiation values were above the saturation level for the equation describing stomatal conductance as a function of radiation (approximately 300 μmol m^{-2} s^{-1}), maximum leaf-to-air humidity deficit was 32 g m^{-3} during this period and stomatal conductance was not reduced at high levels of photosynthetically active radiation. The rapid decline in leaf conductance after 1400 EST on 28 August is the result of a decline in radiation below the saturation point. The increased leaf-to-air humidity deficit and resulting reduction in leaf conductance led to leaf temperatures that were 5 to 6 °C above air temperatures during the middle of the day on 30 July (Figure 5.36). On the 28 August, leaf temperatures were much closer to air temperatures throughout the day.

At the lower evaporative demand on 28 August maximum transpiration continued for about one-half day longer at all levels of irrigation than

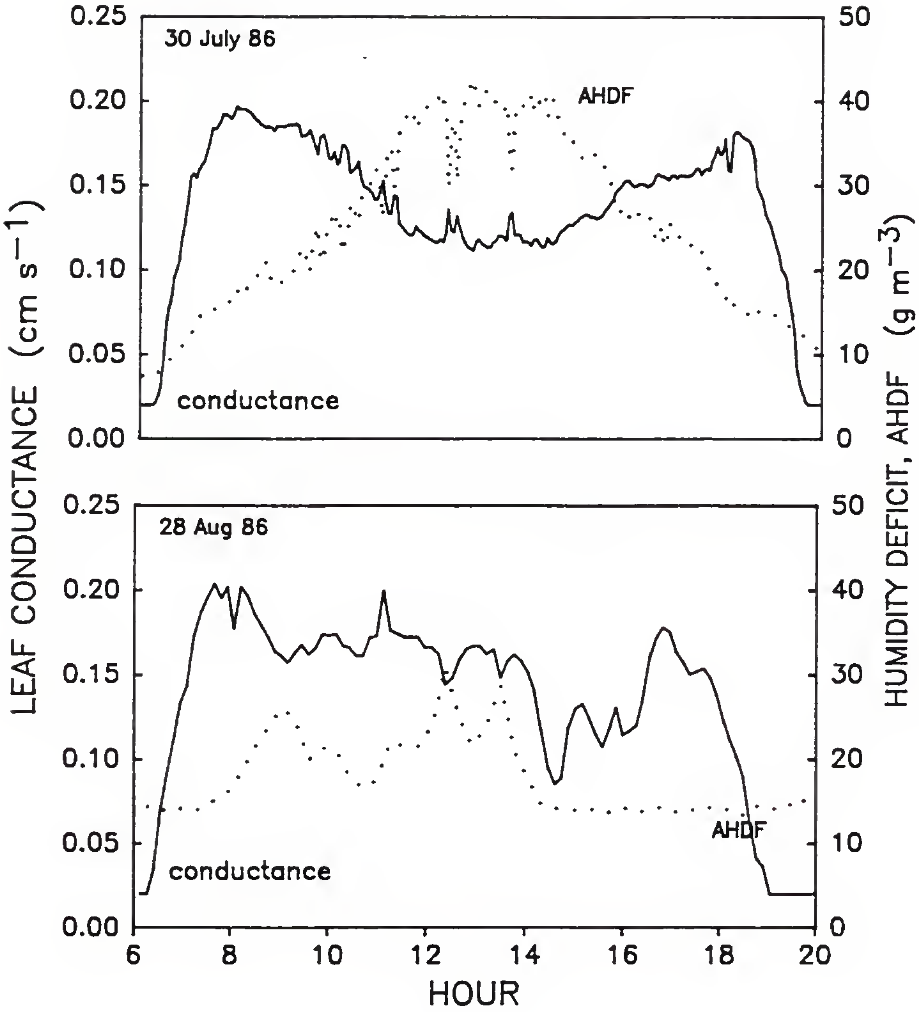


Figure 5.35 Leaf-to-air absolute humidity deficits and leaf conductance of fully irrigated citrus trees on Parkwood variant fine sandy loam under high evaporative demand conditions (30 July) and reduced evaporative demand conditions (28 August).

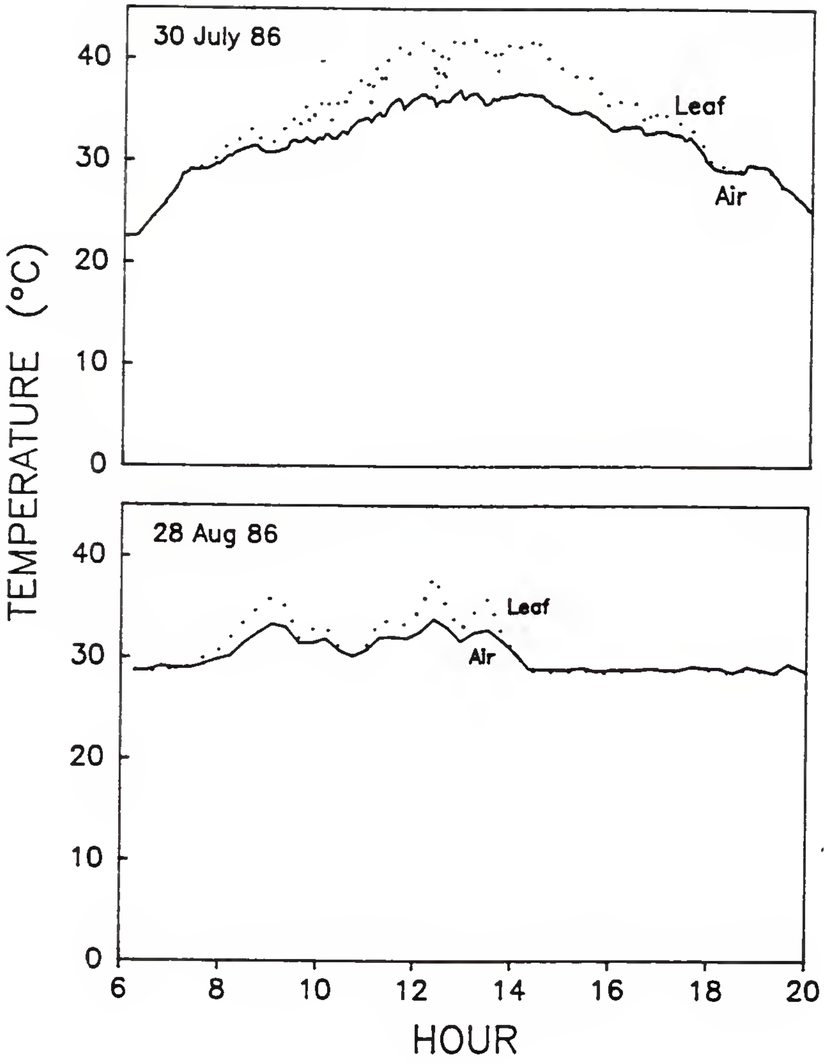


Figure 5.36 Simulated air temperatures and leaf temperatures of fully irrigated citrus on Parkwood sandy loam on 30 July and 28 August.

under evaporative demand conditions on 30 July. On the Parkwood sandy loam transpiration of the one-quarter irrigated citrus tree on 30 July declined precipitously by the midmorning of the fourth day (Figure 5.25) but on the 28 August it did not fall until the morning of the fifth day (Figure 5.37). On the Astatula fine sand, transpiration fell by early morning of the third day on 30 July (Figure 5.26) and on the 28 August water use of the one-quarter irrigated trees fell by late afternoon of the third day (Figure 5.38).

The reduced evaporative demand on 28 August, resulted in reduced shoot demand for water and also in smaller differences in water use rates of citrus tree on the two different soil types. Under reduced evaporative demand conditions, transpiration rates of citrus trees on Astatula soil were nearly the same as those of trees on the Parkwood sandy loam, indicating that the Astatula soil was capable of maintaining flux rates required for maximum transpiration (Figures 5.37 and 5.38).

Differences in water potential gradients around the roots at the two levels of root-length density and evaporative demand indicate that in trees with only one-half or one-quarter of their rooting volume irrigated, the increase in root-length density from 0.12 to 1.0 cm cm^{-3} was more effective in preventing water depletion in the vicinity of the roots than was the decrease in evaporative demand from 30 July to 28 August. Soil water potential gradients on the Parkwood soil at low evaporative demand and low root length density in the 2/4 and 1/4 rooting volume irrigated tree were much larger than those that occurred when both evaporative demand and root length density were high (Figures 5.39 and 5.40).

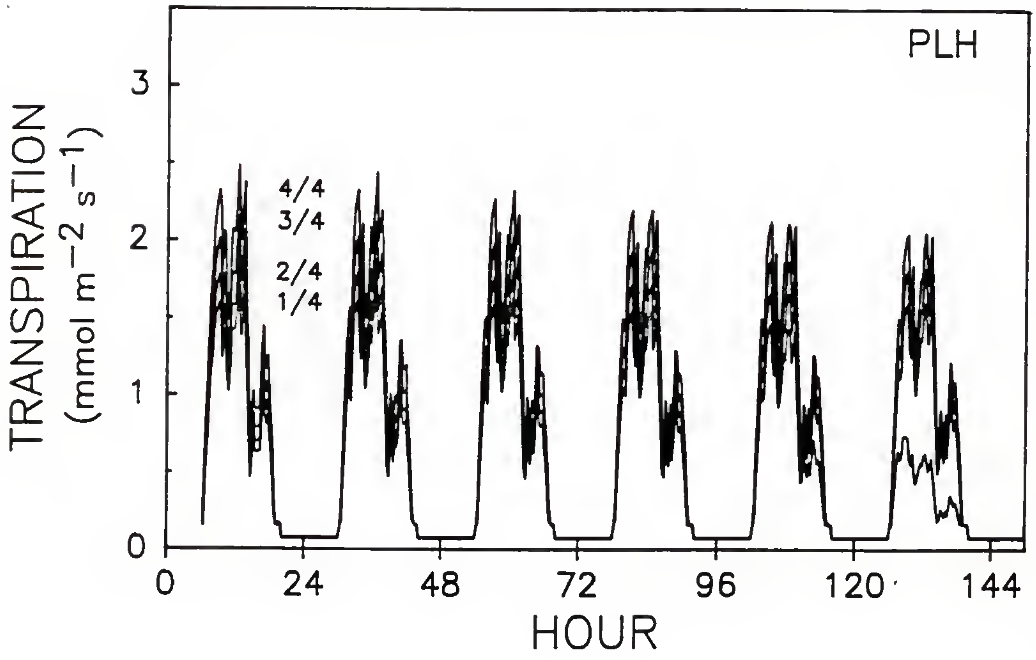


Figure 5.37 Simulated transpiration rates of citrus on Parkwood fine sandy loam (P) at the low dry-bulb temperature (L) and high root length density (H), with 4/4, 3/4, 2/4 or 1/4 of the rooting volume irrigated.

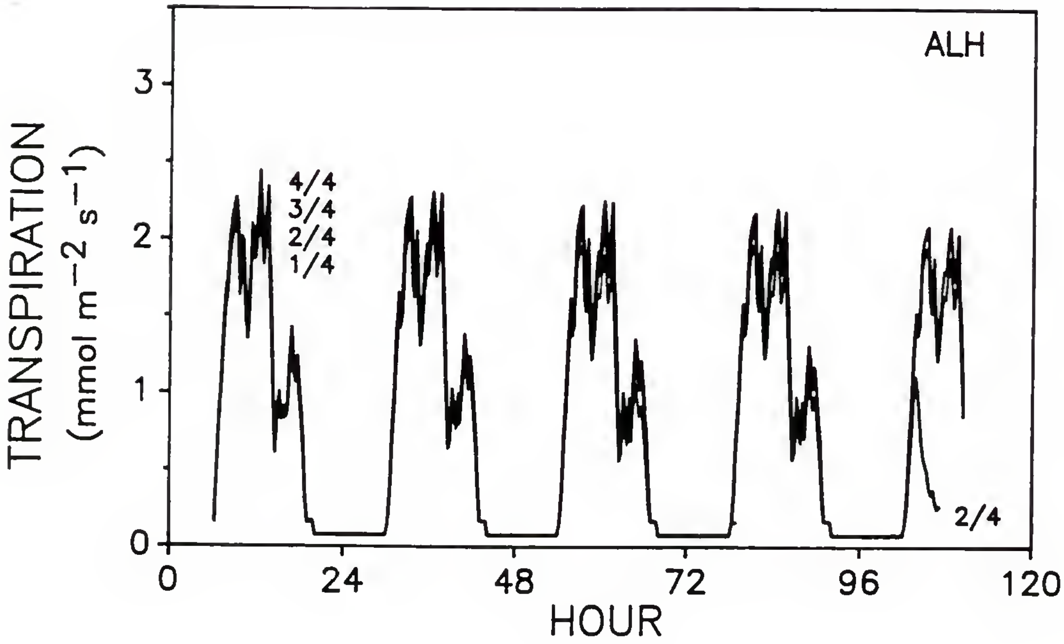


Figure 5.38 Simulated transpiration rates of citrus on Astatula fine sand (A) at the low dry-bulb temperature (L) and high root length density (H), with 4/4, 3/4, 2/4 or 1/4 of the rooting volume irrigated.

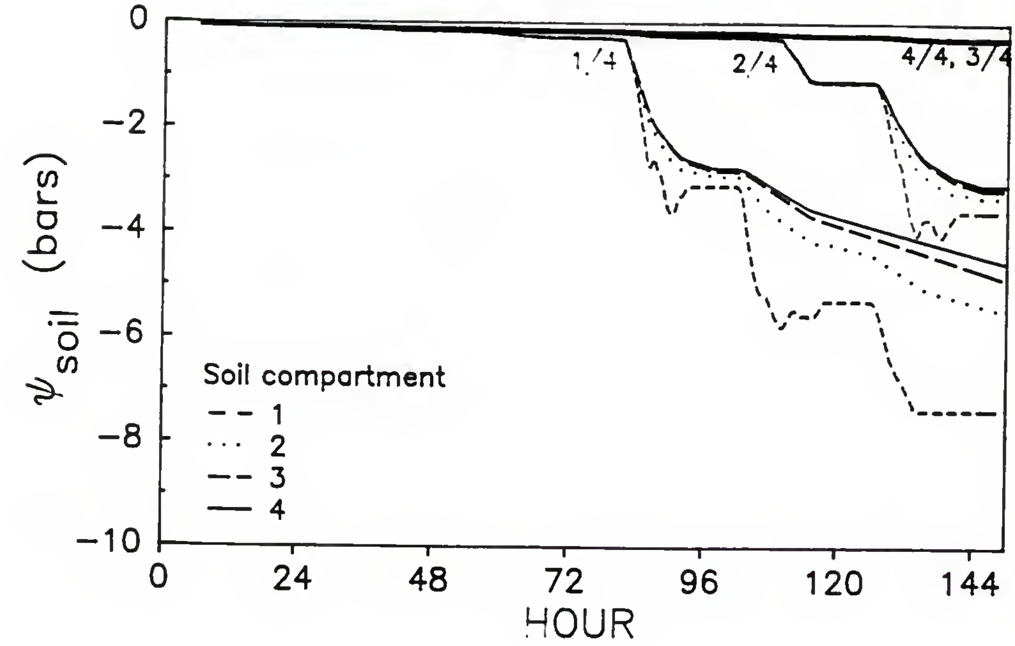


Figure 5.39 Simulated soil water potentials in the cylindrical compartments surrounding the roots of citrus trees on Parkwood sandy loam (P) at the low dry-bulb temperature (L) and low root length density (L), with 4/4, 3/4, 2/4 or 1/4 of the rooting volume irrigated.

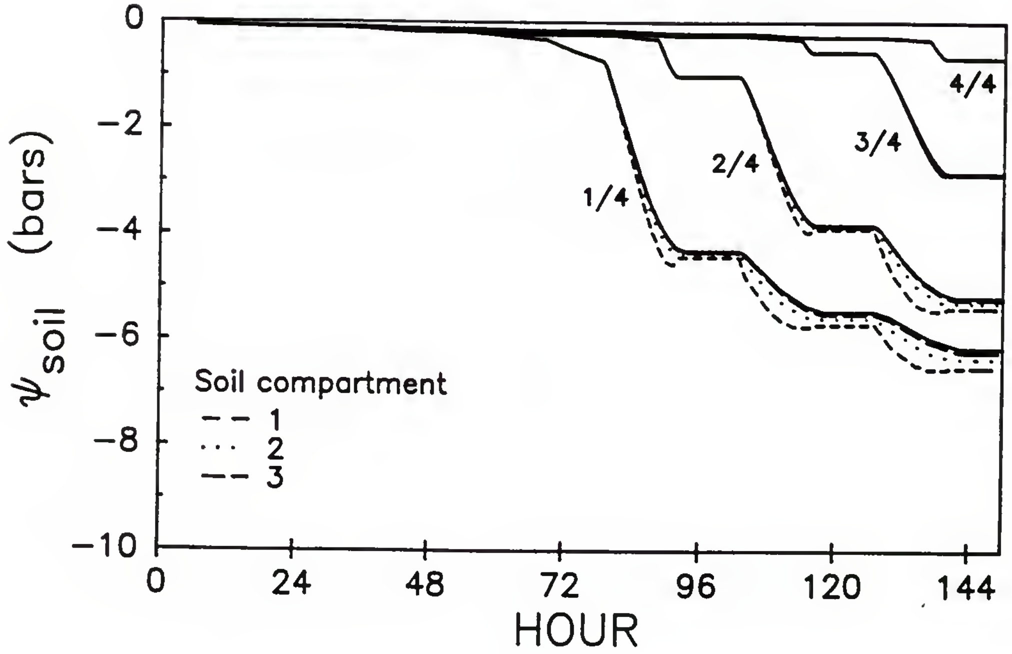


Figure 5.40 Simulated soil water potentials in the cylindrical compartments surrounding the roots of citrus trees on Parkwod fine sandy loam soil (P) at the high dry-bulb temperature (H) and high root-length density (H), with 4/4, 3/4, 2/4 or 1/4 of the rooting volume irrigated.

Total Water Use as Affected by the Soil, Air and Plant Parameters

Total water used by citrus trees over the simulated period at each level of irrigation on Parkwood and Astatula soils as evaporative demand and root length density were varied are summarized in Table 5.2. Water use was greatest for fully irrigated plants at each level of evaporative demand and root length density. At each level of evaporative demand, water use of fully and three-quarters irrigated plants was greater at the low root-length density and may simply reflect the fact that there was a greater volume of soil,and thus volume of available water. In the one-half and one-quarter irrigated treatments, water use at each level of evaporative demand was greater at the high root-length density than at the low root-length density. At each level of root-length density, water use was greatest at high evaporative demand and indicates that transpiration increased with increasing demand, despite reduction of leaf conductance, as the leaf-to-air humidity difference increased. In summary, on both soils the greatest percentage reduction in transpiration rates of partially irrigated trees relative to those of fully irrigated trees as dry-bulb temperature and root length density were varied occurred in the order:
high dry-bulb temperature,low root length density > low dry-bulb temperature,low root length density > high dry-bulb temperature,high root length density > low dry-bulb temperature,high root length density.

DISCUSSION

The results of the simulation revealed a number of areas where understanding of the factors influencing water use by plants with only a

Table 5.2 Total water used by fully irrigated and partial root volume

irrigated (RVI) citrus trees at two levels of dry-bulb temperature (DBT) and root length density (RLD) on Parkwood variant fine sandy loam and Astatula fine sandy.

DBT	RVI	Low RLD	High RLD
		kg	kg
		Parkwood variant fine sandy loam (6 days)	
High	4/4	9.67	8.83
	3/4	8.05	7.65
	2/4	5.86	6.23
	1/4	3.61	4.05
Low	4/4	7.73	6.84
	3/4	6.45	5.97
	2/4	5.36	5.03
	1/4	3.29	3.62
		Astatula fine sand (4.5 days)	
High	4/4	8.97	8.71
	3/4	7.23	7.06
	2/4	5.22	5.44
	1/4	3.30	3.74
Low	4/4	7.85	7.89
	3/4	6.83	6.72
	2/4	4.14	5.19
	1/4	3.45	3.26

portion of their root system wetted is lacking. Foremost among these was the expression describing integration of water status of the soil in contact with the entire root system. The manner in which a plant integrates or measures the water status of the soil in contact with its root system is an important yet poorly defined aspect of plant response to partial irrigation. The methods used in WATFLW for calculating the effective soil water potential are not related directly to any physiological processes determining water loss from citrus trees but rather, represent hypotheses of the phenomenological relationship between leaf conductance and soil water status.

Typically, models of water movement through the soil and plant calculate leaf water potential as the integrator of soil water status. The lack of an apparent, unique relationship between leaf conductance and leaf water potential formed part of the basis for not choosing this approach in WATFLW. The model incorporates the assumption that the major resistance to water flow in the soil-plant system lies in the soil and that leaf conductance can be related directly to soil water status in the vicinity of the roots. For this reason it was not necessary to calculate plant resistance to water uptake or an indicator of plant water status such as leaf water potential. Still, some expression is needed to describe integration of the water status of the soil in the vicinity of the roots throughout the root zone. Herein lies the appeal of the use of leaf water potential in the expression for stomatal conductance. Correlation of leaf conductance to leaf water potential may be more appropriate for a woody species, such as citrus, than for herbaceous species due to greater resistances to water movement throughout the plant. For this reason, leaf xylem water potential might be more representative of water potential throughout the leaf, including that of the guard cells.

Aside from considerations of the physical variables determining water movement in the system, a separate body of literature proposes that leaf conductance to water vapor and water use of plants is closely related to water status of the rooting volume in a way not mediated by changes in leaf water status but rather through the promotion or inhibition of chemical signals that originate in the root (Bates and Hall, 1981; Blackman and Davies, 1985; Gollan et al., 1986; Davies et al., 1989). Jones (1983) stated that the status of water in the vicinity of the roots is an important indicator of the water status of the plant and recommended a procedure for calculating the effective soil water potential at the root surface of transpiring plants. It is evident that such a procedure would be especially useful in situations where stomatal closure succeeds in maintaining leaf water potential relatively constant. Knowledge of soil water status in the vicinity of roots would also be important in understanding the production or inhibition of plant growth regulators.

The concept of inhibition or promotion in the roots of chemical stress signals which influence leaf conductance is an intriguing one that seems applicable to partially irrigated root systems. The results of sensitivity analyses of the method used to calculate the effective soil water potential indicate that consideration of the nonirrigated portions of soil resulted in reduced leaf conductance compared to leaf conductance when the effective soil water potential was based on irrigated portions of soil only. Reduced leaf conductance resulted in lower water use rates which appeared to more closely reflect actual transpiration rates. But there is little basis for assuming that the relationship between growth regulators and the portion of rooting volume irrigated is linear as it was described in WATFLW. At this point it is unclear what the relative contribution of the physical status of water in the plant and the metabolic signals of stress originating in the root to stomatal activity may be or how to express these relationships quantitatively. The deficiency of the model in this area high lights an area of uncertainty and lack of understanding in the general field of plant water relations.

The use of lower water potentials in nonirrigated portions of the rooting volume on the Parkwood soil compared to the Astatula soil obscured differences in the effect of reduced root volume irrigation on the two different soils. Water potentials in irrigated and nonirrigated portions of soil were initially set to values at field capacity and wilting point, respectively. Because of the greater difference between water potential at these levels on the Parkwood soil than on the Astatula soil, the effective water potential was initially lower on this soil and resulted in lower leaf conductances of partially irrigated plants than on the Astatula soil. Still, it is possible to see that if the same water potential at wilting point had been used on both soils, reductions in leaf conductance and transpiration as the root volume irrigated was reduced would be similar at high levels of soil water content. As water was depleted, the greater water holding capacity and hydraulic conductivity of the Parkwood soil would permit maintenance of maximum transpiration rates for longer periods of time at each level of irrigation compared to the Astatula soil.

A nonproportional relationship between reductions in transpiration and the root volume irrigated was found in simulations and has been reported in several studies of partial irrigation (Lawlor, 1973; Black and West, 1976; Tan et al., 1981; Tan and Buttery, 1982). It may be hypothesized that if the water transporting capacity of the reduced volume of rooting zone is able to maintain the required flux rates then transpiration will be relatively unaffected by the reduction in irrigated roots. Furthermore, if root resistance was the limiting factor to water transport in the soil-root system and was constant over a short time, then the reduction in transpiration should be proportional to reduction in the irrigated portion of roots, i.e., a 50% reduction in irrigated roots should yield a 50% reduction in transpiration. As mentioned before, transpiration typically does not decline proportionally to reduction in root volume irrigated.

It was proposed in several studies (Lawlor, 1972; Aston and Lawlor, 1979; Tan and Buttery, 1982) that the absorption capacity of roots in irrigated portions of soil increases as the portion of roots irrigated is reduced, or as stress on the remaining portion of roots increases, so that transpiration rates remain relatively constant. Because of the short-term nature of these studies it is unlikely that an increase in conductance of the root system was due to an increase in root length in the irrigated soil volume. Such an increase in conductance would have to be explained by an increase in the hydraulic conductivity of the root tissue. But, the hydraulic conductivity of irrigated roots of partially irrigated, containerized citrus trees did not increase as the portion of roots irrigated was reduced (chapter IV).

These results suggest that when the hydraulic conductivity of the rooting medium is high, as it is in water culture or when the soil is near saturation, root resistance determines the rate of water absorption. As evaporative demand or water uptake per unit root length is increased under these conditions, root resistance may decline until a minimum resistance is encountered as suggested by Aston and Lawlor (1979). It may be further reasoned that as soil water is depleted root resistance no longer provides the major factor limiting water transport in the root-soil system. Increasingly, it is capacity of the soil to transport water to the root at greater flux rates that will determine whether transpiration rates are maintained.

The use of a microscopic approach to modeling soil water movement seems justified given the combination of the sandy soils on which citrus is often grown in Florida as well as low root length densities, often lower than 1.0 cm cm^{-3}, of young citrus trees. Although Gardner (1960) indicated that soil water potential gradients in the vicinity of roots would not be significant at water potentials less than -15 MPa, his analysis did not account for variable soil hydraulic conductivity. Hillel (1975) developed a numerical model to calculate water movement to single roots and showed that significant water depletion in the vicinities of roots occurred at less than -15 MPa on a sandy loam soil. Soil water depletion in the vicinity of roots measured with computer assisted tomagraphy closely agreed with values predicted by Hillel's model (Hainsworth and Alymore, 1986). These results support the concept that soil resistance to water movement plays a significant role in controlling water uptake by the plant root even at high soil water potentials. This concept was also supported by results obtained by Tinklin and Weatherly (1968) and Passioura (1980) of plant water loss in relation to soil water status. Whereas the arguments of unrealistically low root length density and high transpiration rates have been directed against the results obtained by Gardner (1960) and Cowan (1965), water potential gradients in the vicinity of roots were obtained with WATFLW using representative values of leaf area, atmospheric evaporative demand and root length density from experimental studies.

The results obtained here indicate that high soil resistance is an important factor limiting water availability to roots of young citrus trees on these soils which may result in appreciable water depletion in the vicinities of roots. But several other processes not included in WATFLW may provide important contributions to water supply to roots on Florida soils. These include: the upward capillary movement of water from high water tables, rainfall and gravity redistribution of water and, under very dry conditions, water vapor transport to roots. Because the root system is constantly changing through growth and loss of roots, description of changes in root-length density and the total rooting volume may be necessary additions to the model if it is used to simulate water use over long periods of time.

The results obtained from the model did not clearly indicate the influence of soil type in determining the fraction of roots that must be irrigated to supply sufficient water to the shoot when soil water content is high. The results do illustrate that as soil water is depleted a greater portion of roots must be irrigated on soils with low water holding capacity and hydraulic conductivities in order to maintain potential transpiration rates. This suggests that on sandy soils it will be critical to schedule irrigation more frequently as the portion of root volume irrigated is reduced. The results also support the hypothesis that evaporative demand and root-length density are parameters that will affect the ability of the partially irrigated citrus trees to obtain sufficient water and that these factors should be given consideration in discussions and recommendations proceeding from partial rooting volume irrigation studies.

Future studies are needed to substantiate assumptions and relations used in the model and validate results of the model. The relationships between citrus leaf conductance and photosynthetically active radiation, leaf-to-air humidity deficit, and soil water potential used in the model were developed from seven different sets of data reported in the literature. These relationships should be developed from data collected under similar conditions and the equation describing citrus leaf conductance to these three environmental factors should be validated with a similar set of data.

While the relationships of leaf conductance to radiation and humidity deficit may be adequately described by the data reported in the literature, the relationship of leaf conductance to soil water potential is a very tentative one, being based on a single set of data reported in the literature. Citrus leaf conductance activity in relation to soil water status, both water potential and volumetric water content, should be evaluated using a range of soils varying in their moisture holding capacity. Further studies are also needed to describe the phenomenological relationship between leaf conductance and soil water status of both partially and fully irrigated citrus trees. This work may provide insights as to how the soil water status is integrated in the plant.

The relationship between shoot water loss and rooting characteristics requires further investigation to determine if root-length density is the most appropriate root parameter to measure. Studies of root permeability along the length of the root may provide a more accurate indication of the effective root length.

It would be valuable to conduct studies on citrus leaf water status and water loss in relation to soil water status, such as those conducted by Tinklin and Weatherly (1968) and Passioura (1980), to gain further evidence of the importance of soil resistance to water movement and water uptake by citrus roots. In conjunction with such studies, the relationship between water use and photosynthesis in citrus trees needs to elucidated. Although water loss may be controlled very effectively in citrus, thus enabling it to grow under arid conditions, low water availability that results in water stress may have pronounced, negative effects on photosynthesis. If so, this would emphasize the need to insure adequate water supply to partially irrigated citrus trees.

CHAPTER VI

CONCLUSIONS

Citrus growth is frequently described as water conservative, largely because of stomatal sensitivity to leaf-to-air humidity differences which results in low, nearly constant, levels of transpiration as atmospheric vapor pressure deficit increases. This behavior was supported by nonlinear increases in transpiration from citrus canopies in controlled-environment growth chambers in both 1985 and 1986 as atmospheric vapor pressure deficit increased. It is widely thought that this characteristic enables citrus to grow well in arid regions or in regions experiencing seasonal drought.

Less well defined is the response of citrus photosynthetic rates to conditions of high evaporative demand, high dry-bulb temperatures, and soil water stress. Carbon dioxide exchange rates of citrus trees on a loam soil in 1985 decreased with soil water depletion when dry-bulb temperatures and vapor pressure deficits were high, but not at the low temperature and vapor pressure deficit. Midday depression of photosynthesis occurred only at low soil water contents in conjunction with high dry-bulb temperatures and vapor pressure deficits. In 1986, midday depression of photosynthesis occurred at all levels of soil water content, dry-bulb temperature or evaporative demand in citrus trees grown on a sandy soil. Although specific components of mesophyll resistance to carbon dioxide fixation were not measured in these studies, it appears that nonstomatal factors played a greater role in reducing photosynthetic rates than did stomatal closure. Furthermore, the hypothesis that nonstomatal factors of carbon dioxide fixation may be sensitive to high temperatures when low soil water content or high evaporative demand cause plant water stress, is a concept that unifies much of the behavior of photosynthetic rates of citrus trees observed in both 1985 and 1986. If such is the case, it would imply that growth and productivity of citrus may be reduced by sensitivity of photosynthetic rates to high temperatures when water stress occurs. It would also emphasize the need to insure that soil water is readily available, to avoid midday reduction of photosynthetic rates.

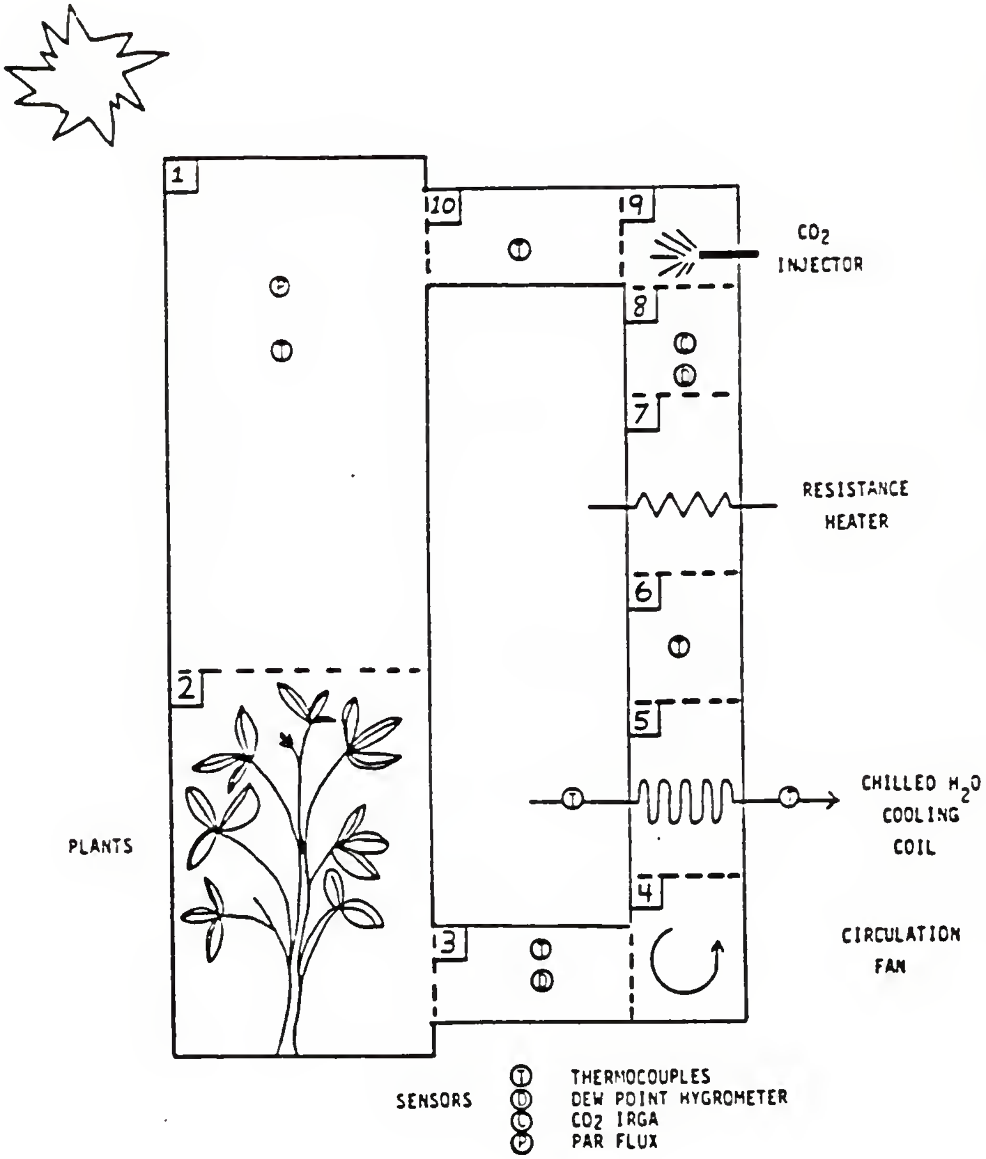
Adequate soil water supply and availability will be determined in part by the portion of rooting volume that is supplied with water. In 1986, the response of young citrus trees to irrigation of 4/4, 3/4, 2/4 or 1/4 of the rooting volume, demonstrated that growth was closely related to the fraction of the rooting volume irrigated. These results concur with results of partial irrigation studies conducted on field-grown trees in Florida. One common factor of many partial irrigation studies that have reported detrimental effects of reduced rooting volume irrigation, is that trees were grown on coarse-grained soils. This fact suggests that soil type may be an important determinant of the success of partial irrigation practices.

Simulation of soil water movement and plant water use was employed to estimate the role that soil type plays in influencing the ability of partial irrigation practices to supply adequate water to the plant. Results of simulations suggest that the water conducting properties of the soil strongly influence water availability in the vicinity of roots. Furthermore, reduction in the portion of rooting volume irrigated resulted in reduction of predicted water availability in the vicinity of roots to a greater extent on a sandy soil than on a sandy loam soil. Increase in evaporative demand over the range studied also reduced predicted water content in the rooting zone, but to a lesser degree than did the decrease in root-length density. The decrease in water content in the vicinity of roots resulted in a reduction in simulated leaf conductance and transpiration rates.

A number of untested assumptions were used to describe plant processes in the model WATFLW and require further experimental work in order to substantiate or disprove them. Foremost among these is the expression combining the influence of radiation, humidity deficit, and soil water potential on leaf conductance, as well as the manner in which the effective soil water potential is derived. At present, the description of these processes in the model WATFLW represents a working hypothesis of how water movement in the soil and water loss from a citrus tree are influenced by the portion of roots irrigated, soil type, evaporative demand, and root-length density.

APPENDIX A

A SIDE-VIEW SCHEMATIC OF AN ENVIRONMENTALLY CONTROLLED PLANT GROWTH CHAMBER AND ASSOCIATED DUCTWORK. THE CHAMBER IS SUBDIVIDED INTO TEN NUMBERED COMPARTMENTS, EACH CONTAINING CONTROL ELEMENTS, SENSORS OR OTHER KEY SYSTEM COMPONENTS. AIR CIRCULATES INTO THE GROWTH CHAMBER FROM THE UPPER DUCT (10) AND EXISTS INTO THE LOWER DUCT (3).



APPENDIX B

CITRUS STUDY, SPAR CHAMBERS 1985: ENVIRONMENTAL CONDITIONS[*].

Date	Time (EST)	Maximum DBT (°C)	Constant DPT (°C)	CO_2 (μmol mol^{-1})
Apr 9	0900	29	14	330
" 18	1530	37	22	330
" 21	1915	29	14	330
" 25	1255 - 1455	37	22	330
	1500 - 1820	29	14	330
	1825	37	22	330
" 29	0725	37	22	840
" 30	0800	29	14	840
May 4	0755	37	22	840
" 10	1430	37	22	330
" 14	1200	24	10	330
" 15	0700	DBT switched to square wave control.		
" 20	0800	37	22	330
" 24-27		Heater failure in Swingle chamber, different DBT/DPT controls in both chambers.		
" 31	0900	37	22	840
Jun 05	0830	37	22	330
" 7	1520	Flooded citrus trays.		
" 17	0755	Removed citrus from SPAR chambers.		

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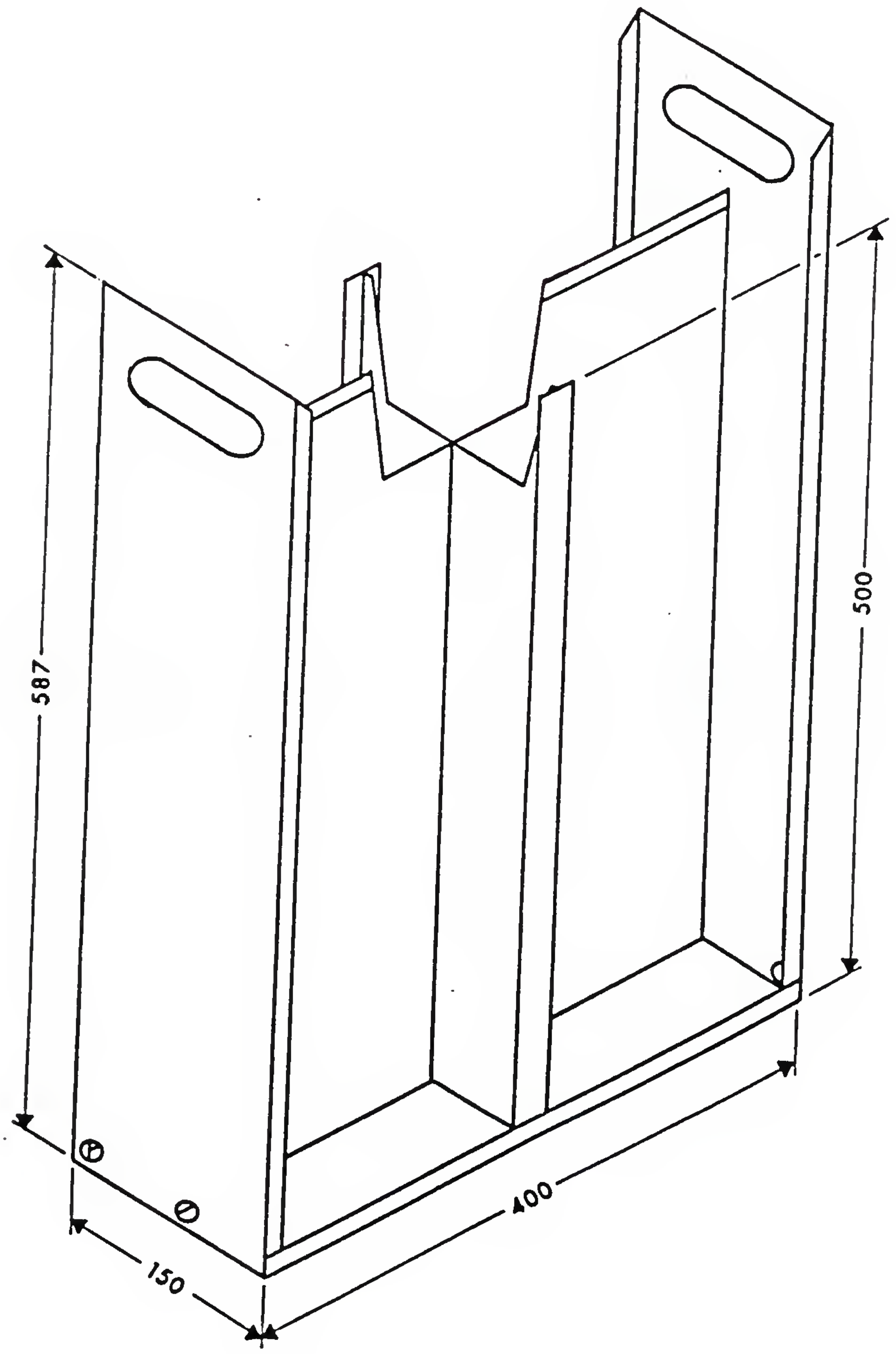
[*] Night time DBT/DPT control points for the 24/10, 29/14 and 37/22 °C DBT/DPT treatments were, 14/6, 16/14 and 22/14 °C, respectively.

APPENDIX C

DIAGRAM OF THE FOUR-PART SPLIT-ROOT CONTAINERS USED FOR CITRUS TREES IN THE PARTIAL ROOT-VOLUME IRRIGATION STUDY IN 1986 (DIMENSIONS IN mm).



APPENDIX D

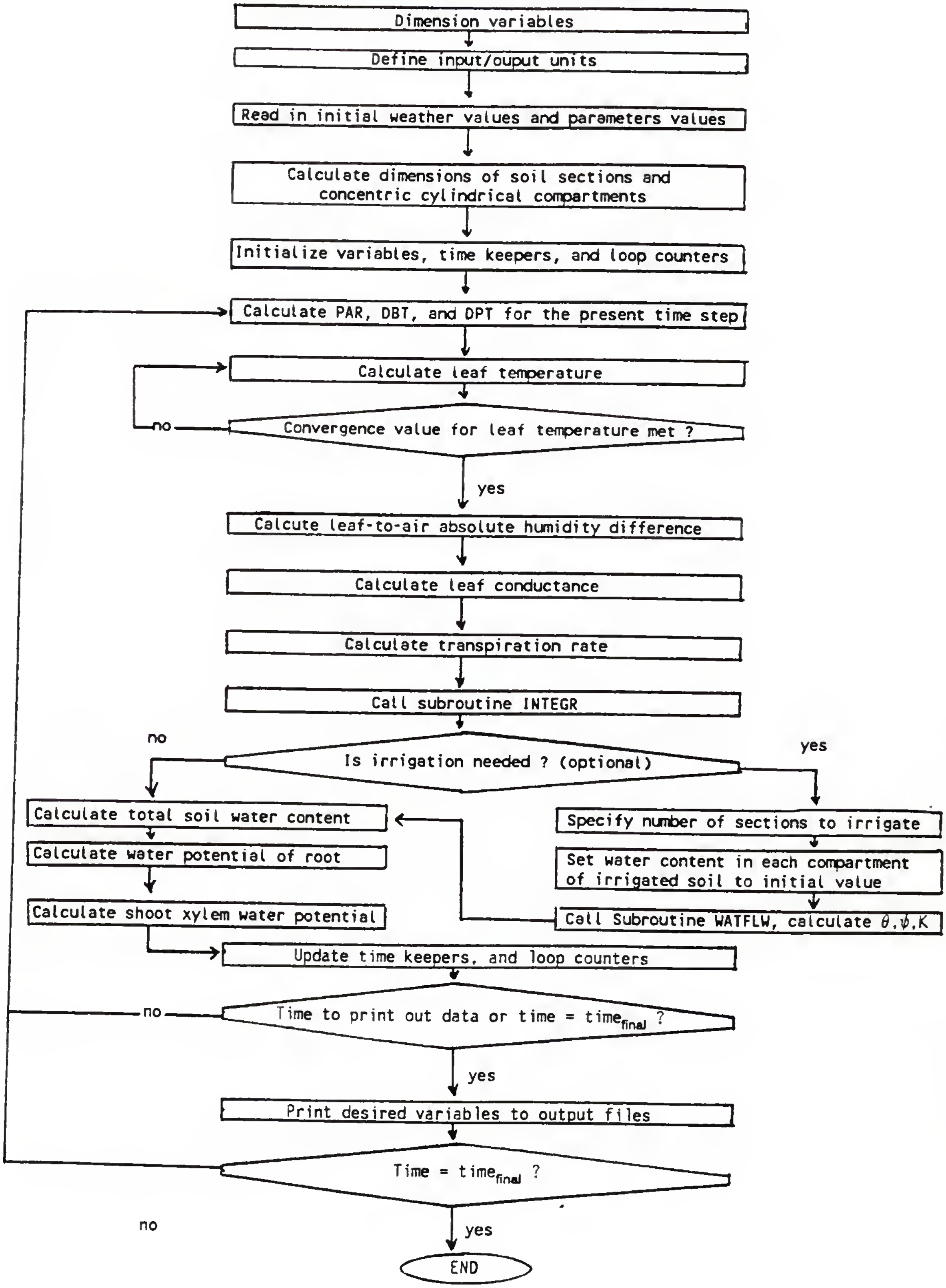
SCHEDULE OF CITRUS ESTABLISHMENT IN 1985 AND CONTROLLED ENVIRONMENT CHAMBER TREATMENTS IN 1986.

Date	Event
16-22 Aug 85	Acquired citrus treelings. Pruned roots and placed treelings in rooting trays to establish split-root systems.
15 Feb 86	Began transferring citrus trees from the rooting trays to split-root containers.
01 May 86	St. Augustine grass seed planted in 21 containers.
25 May 86	Harvested 6 plants for evaluation of split-root technique.
14 Jun - 03 Aug 86	Citrus trees placed in all SPAR chambers. Environmental control setpoints for low DBT/VPD ambient CO_2 conditions. DBT = 29/25 °C (day/night) DPT = 18/14 °C CO_2 = 340 μmol mol^{-1}
14-24 Jun 86	Citrus treelings maintained under well irrigated conditions, i.e., irrigated in all compartments of containers.
25 Jun 86	Initiated partial irrigation treatments.
04-10 Aug 86	Environmental control setpoints for high DBT/VPD, ambient CO_2 conditions. DBT = 37/25 °C DPT = 22/14 °C CO_2 = 340 μmol mol^{-1}
11-19 Aug 86	Environmental control setpoints for high DBT/VPD, elevated CO_2 conditions. DBT = 37/25 °C DPT = 22/14 °C CO_2 = 880 μmol mol^{-1}
20-25 Aug 86	Environmental control setpoints for low DBT/VPD, elevated CO_2 conditions. DBT = 29/25 °C DPT = 18/14 °C CO_2 = 880 μmol mol^{-1}

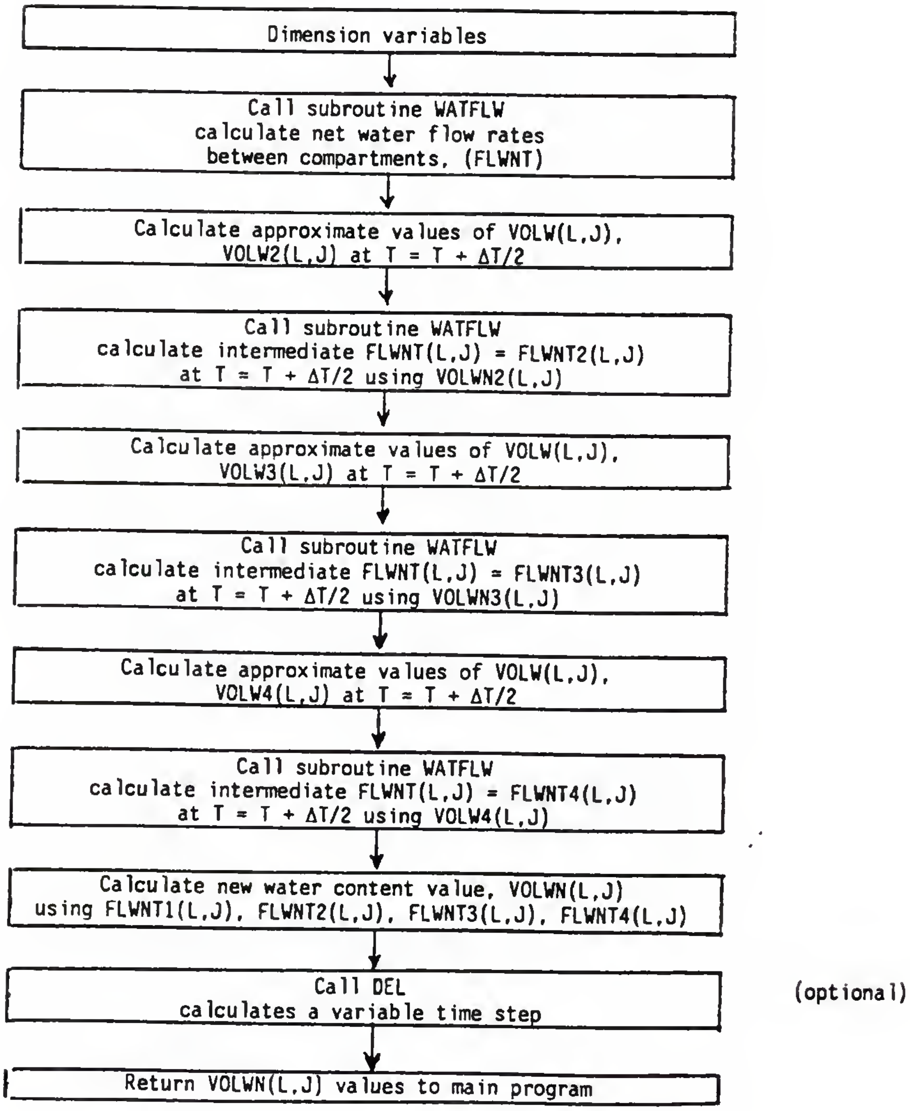
26 Aug - 13 Oct 86	Environmental control setpoints for low DBT/VPD, ambient CO_2 conditions. DBT = 29/25 °C DPT = 18/14 °C CO_2 = 340 μmol mol^{-1}
15 Sep 86	Began removing plants form SPAR chambers for biomass and root hydraulic conductivity measurements.
13 Oct 86	Finished sampling plants; all plants removed from chambers.

APPENDIX E

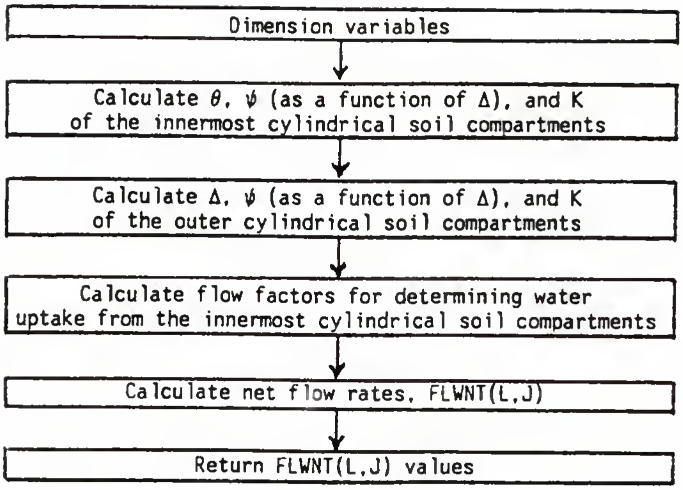
FLOW DIAGRAM OF THE CITRUS WATER FLOW MODEL 'WATFLW'


Dimension variables
Define input/ouput units
Read in initial weather values and parameters values
Calculate dimensions of soil sections and concentric cylindrical compartments
Initialize variables, time keepers, and loop counters
Calculate PAR, DBT, and DPT for the present time step
Calculate leaf temperature
no
Convergence value for leaf temperature met ?
yes
Calcute leaf-to-air absolute humidity difference
Calculate leaf conductance
Calculate transpiration rate
Call subroutine INTEGR
no
Is irrigation needed ? (optional)
yes
Calculate total soil water content
Calculate water potential of root
Calculate shoot xylem water potential
Specify number of sections to irrigate
Set water content in each compartment of irrigated soil to initial value
Call Subroutine WATFLW, calculate θ,ψ,K
Update time keepers, and loop counters
no
Time to print out data or time = time_final ?
yes
Print desired variables to output files
Time = time_final ?
no
yes
END

SUBROUTINE INTEGR


Dimension variables
Call subroutine WATFLW
calculate net water flow rates
between compartments, (FLWNT)
Calculate approximate values of VOLW(L,J),
VOLW2(L,J) at T = T + ΔT/2
Call subroutine WATFLW
calculate intermediate FLWNT(L,J) = FLWNT2(L,J)
at T = T + ΔT/2 using VOLWN2(L,J)
Calculate approximate values of VOLW(L,J),
VOLW3(L,J) at T = T + ΔT/2
Call subroutine WATFLW
calculate intermediate FLWNT(L,J) = FLWNT3(L,J)
at T = T + ΔT/2 using VOLWN3(L,J)
Calculate approximate values of VOLW(L,J),
VOLW4(L,J) at T = T + ΔT/2
Call subroutine WATFLW
calculate intermediate FLWNT(L,J) = FLWNT4(L,J)
at T = T + ΔT/2 using VOLW4(L,J)
Calculate new water content value, VOLWN(L,J)
using FLWNT1(L,J), FLWNT2(L,J), FLWNT3(L,J), FLWNT4(L,J)
Call DEL
calculates a variable time step
(optional)
Return VOLWN(L,J) values to main program

SUBROUTINE WATFLW


Dimension variables
Calculate θ, ψ (as a function of Δ), and K of the innermost cylindrical soil compartments
Calculate Δ, ψ (as a function of Δ), and K of the outer cylindrical soil compartments
Calculate flow factors for determining water uptake from the innermost cylindrical soil compartments
Calculate net flow rates, FLWNT(L,J)
Return FLWNT(L,J) values

APPENDIX F

FORTRAN SOURCE CODE FOR THE CITRUS WATER USE MODEL, 'WATFLW'

VARIABLE DEFINITIONS

Atmospheric variables

Input variables
rn: net radiation (W m^{-1})
dbt: dry-bulb temperature (°C)
dpt: dewpoint temperature (°C)
dbtk: dry-bulb temperature (°K)
dptk: dewpoint temperature (°K)

Calculated variables
ahta: absolute humidity at air temperature (g m^{-3})
ahtl: absolute humidity at leaf temperature (g m^{-1})
ahdf: absolute humidity difference between leaf and air
deltmp: leaf to air temperature difference (°C)
eata: partial pressure of water vapor in air (Pa)
esta: saturation vapor pressure at air temperature (Pa)
estl: saturation vapor pressure at leaf temperature (Pa)
estlest: saturation vapor pressure at estimated leaf temp (Pa)
gam: psychrometric constant (Pa $°C^{-1}$)
gslw: total stomatal conductance (m s^{-1})
lam: latent heat of vaporization (J kg^{-1})
par: photosynthetically active radiation (μmol m^{-2} s^{-1})
rsah: air resistance to sensible heat transfer (s m^{-1})
rsaw: boundary layer resistance to water vapor (s m^{-1})
rscw: cuticular resistance to water vapor loss (s m^{-1})
rshr: rsah + rsar
s: slope of saturation vapor pressure over temp (Pa $°C^{-1}$)
test: variable to test convergence of tl calculation
tl: temperature of leaf (°C)
tlest: estimated leaf temp used in calculation of s (°C)
tlestk: estimated leaf temp (°K)
totr: total transpiration (g m^{-2} s^{-1})
tr: transpiration rate (mmol m^{-2} s^{-1})
vpd: vapor pressure deficit of the air (Pa)

Parameters
e: emissivity of leaves
d: leaf width (m)
la: leaf area (cm^2)
u: velocity of wind (m s^{-1})

Constants
cp: specific heat of air at constant pressure (J kg^{-1} $°C^{-1}$)
da: density of air (kg m^{-3} at 30 °C)
mwma: ratio of molecular wt of water to molecular wt of air
mwt: molecular weight of water (g)
p: pressure of air (Pa)
r: universal gas constant (Pa m^3 mol^{-1} $°K^{-1}$)
sig: Stefan Boltzman constant (W m^{-2} $°K^{-1}$)

Soil variables

Calculated

areac(l,j): peripheral area of each compartment (cm^2)
cond(l,j): effective hydraulic conductivity for each flow compartment ($cm\ s^{-1}$)
csac(l): cross sectional area of the entire soil cylinder surrounding the root (cm^2)
csaf(l): cross sectional area of the first soil compartment (cm)
dr(l,j): radial length of flow for each flow compartment (cm)
flw(l,j): rate of water flow between soil compartments ($g\ s^{-1}$)
nflw(l,j): difference between inflow and outflow of water for each soil compartment ($g\ s^{-1}$)
potgd(l,j): water potential difference between compartments (cm H_2O)
poth(l,j): water potential for each soil compartment (cm H_2O)
potrt: root water potential
rad(l,1): radius of the root (cm)
rad(l,j): radii of the concentric soil compartments (cm)
radc(l): overall radius of the shell of soil surrounding the roots in layer (l) (cm)
rl(l): root length in soil layer l (cm)
rssl(l): soil resistance to water flow of the innermost soil compartment in soil layer l ($s\ cm^{-1}$)
rtrs(l): root resistance to water in soil layer l
tcr(l,j): thickness of each soil compartment (cm)
theta(l,j): volumetric water content in each soil compartment ($cm^3\ cm^{-3}$)
thkl(l): thickness of soil layer l (cm)
trl: total root length (cm)
tsvol: total soil volume (cm^3)
tsvolc(l): total volume of compartments in soil layer l (cm^3)
tvolw: total volume of water in the irrigated soil (cm^3)
vcc(l,j): volume of each soil compartment (cm^3)
volw(l,j): volume of water in each soil compartment (cm^3)

Parameters

alpha: calculated parameter for Van Genuchten's equation
depth: vertical thickness of total soil volume (cm)
di: diameter of total soil volume (cm)
thetai: initial volumetric water content of the soil ($cm\ cm^{-3}$)
kmp: number of cylindrical concentric compartments surrounding the root
kkmp: kmp + 1
vm: calculated parameter for Van Genuchten's equation
vn: calculated parameter for Van Genuchten's equation
ritr: relative increase in thickness of cylindrical compartments
rld(l): root length density in each soil layer ($cm\ cm^{-3}$)
rpf: root permeability factor

Other variables

delt: time increment value for simulation (s)
i: overall counter variable

```
           j: array variable for soil compartments
          tf: final time value for simulation (s)
          to: initial time value for simulation(s)

 DECLARE VARIABLES
        real lam, mwma, mwt, la, cond(4,9), flw(4,9), volwi(4,9)
        real poth(4,9), radc(4), rad(4,9), rssl(4), tcr(4,9), volw(4,9)
        real theta(4,9), thetar(4,9), potrt(4), potgd(4,9)
        real thkl(4), rl(4), potl(4), potlst(4,9), potlf(4)
        real res(4,9), vol(4), iramt(4,9), flwnt(4,9), volw5(4,9)
        real tvolsc(4), csaf(4), csac(4), potb(11), thtb(11)
        real capf(4,9), potf(4,9), thetai(4,9)

        double precision timet, delt

        integer i, iday, int, j, kmp, kkmp, l, tout, n, lay, irr
        character*20 soltyp

        common /amin/ l, j, lay, kmp, kkmp, condc(4,9), pothc(4,9), wpt
        common /amin2/ thetarc(4,9), thetac(4,9), flwc(4,9), flwnt5(4,9)
        common /init/ to, tf, volw1(4,9), volwn(4,9)
        common /soldi/ rld(4), vcc(4,9), dr(4,9), areac(4,9), vm, tran
        common /solparm/ sat, resid, alpha, vn, satk

        data da,mwt,cp/1.164,18.016,1004.880/
        data r,ri,p,mwma/8.314,3.14159,101300.,0.622/

 OPEN INPUT AND OUTPUT FILES
        open(unit=08,file='hidbt.dat')
        open(unit=09,file='rad.dat')
        open(unit=10,file='misc.dat')
        open(unit=11,file='volw1.dat')
        open(unit=12,file='thet1.dat')
        open(unit=13,file='poth1.dat')
        open(unit=14,file='cond1.dat')
        open(unit=15,file='tran.dat')
        open(unit=21,file='volw4.dat')
        open(unit=22,file='thet4.dat')
        open(unit=23,file='poth4.dat')
        open(unit=24,file='cond4.dat')

        read(8,*)par1,dbt1,dpt1
        read(17,*)to,tf,delt,pout
        read(17,*)bet,href,u,tplw
        read(17,*)la,rscw,d,rsrt
        read(17,*)rld(1),rld(2),rld(3),rld(4)
        read(17,*)soiltyp
        read(17,*)di,depth,lay,kmp,ritr
        read(17,*)alpha,vn,satk,fc,wpt
        read(17,*)thetai(1,1),thetai(1,2),thetai(1,3),thetai(1,4)
        read(17,*)thetai(2,1),thetai(2,2),thetai(2,3),thetai(2,4)
        read(17,*)thetai(3,1),thetai(3,2),thetai(3,3),thetai(3,4)
```

```
      read(17,*)thetai(4,1),thetai(4,2),thetai(4,3),thetai(4,4)
      read(17,*)sat,resid,irig
      read(17,*)ra,rb,rc

CALCULATE DIMENSIONS OF SOIL COMPARTMENTS
      kkmp = kmp + 1
C     calculate the total volume of irrigated soil (cm³)
      tsvol = ((pi*(di*0.5)**2)*depth

C     calculate the thickness and volume of each soil layer as well as
C     root length in each layer and total root length
      trl = 0.0
      do 202 l = 1,lay
         thkl(l) = depth/lay
         vol(l) = (pi*(di*0.5)**2)thkl(l)
         rl(l) = rld(l)*vol(l)
         trl = trl + rl(l)
  202 continue

C     calculate radius of overall soil cylinder in each soil layer
      do 204 l =1,lay
        radc(l) = (sqrt(1./(rld(l)*pi)))
  204 continue

C     assign uniform root radius in all soil layers
      do 205 l = 1,lay
         rad(l,1) = 0.075
  205 continue

C     calculate dimensions of the innermost soil compartment in each
C     soil layer
      do 206 l = 1,lay
         tcr(l,1) = ((radc(l)-rad(l,1))*(1 - ritr)/(1. - ritr**kmp))
         areac(l,1) = (2.*pi*rad(l,1)*(rkd(l)*tsvol))
         dr(l,1) = (.5*tcr(l,1))
  206 continue

C     calculate dimensions of the outer soil compartments, radius,
C     thickness, area, volume and flow length of each compartment
      do 210 l = 1,lay
         do 208 j = 2,kmp
            tcr(l,j) = (ritr*tch(l,j-1))
            rad(l,j) = (rad(l,j-1) + tcr(l,j-1))
            areac(l,j) = (2.*pi*rad(l,j)*(rld(l)*tsvol))
            dr(l,j) = ((tcr(l,j-1) + tcr(l,j))*0.5)
  208    continue
  210 continue

      do 209 l = 1,lay
         rad(l,kkmp) = rad(l,kmp) + tcr(l,kmp)
  209 continue
```

```
C     calculate volume of soil compartments
      do 211 l = 1,lay
         tvolsc(l) = 0.0
  211 continue
      do 214 l = 1,lay
         do 212 j = 1,kmp
         vcc((l,j) = (pi*(rad(l,j+1)**2-rad(l,j)**2))*(rld(l)*vol(l))
         tvolsc(l) = tvolsc(l) + vcc(l,j)
  212 continue
C     calculate cross-sectional area of the first soil compartment
      csaf(l) = (pi*(rad(l,2)**2-rad(l,1)**2))

C     calculate cross-sectional area of the entire soil cylinder
      csac(l) = (pi*(radc(l)**2 - rad(l,1)**2))
  214 continue

C     calculate initial volume of water in each layer and compartment
      do 220 l = 1,lay
         do 216 j = 1,kmp
            volwi(l,j) = thetai(l,j)*vcc(l,j))
  216 continue
  220 continue

C     calculate m for Van Genuchten's equation
      vm = 1. - (1./vn)

C     calculate initial thetal and poth for the first soil compartment
      do 232 l = 1,lay
         do 232 j = 1,kmp
            theta(l,j) = thetai(l,j)
  232 continue

BEGIN DYNAMIC PORTION OF THE MODEL
      do 234 l = 1,lay
         do 234 j = 1,kmp
            volw(l,j) = volwi(l,j)
            flw(l,j) = 0.0
  234 continue

C     set initial values of counter variables
      ispy = 0
      idd = 0
      timet = 0.0d+00
      start = 6.0
      hour = 6.0
      irnd = 1
      icnt = 0
      id = 0
      mned = nint(60./delt)
      min = 0
      iday = 0
      tl = dbt - 0.1
```

```
       rslw = rscw/2.
       gslw2 = 1./rslw
       cumtr = 0.0
       potfac = tlulin(thetai(1,1),11)
       rplw = 1.0
       write(6,20)
    20 format(3x,'dynamic beginning...')
       goto 1000

CALCULATE ATMOSPHERIC VARIABLES
   900 continue
       rewind 8
       iday = iday + 1
       hour = 6.0
       write(6,505)iday
   505 format(3x,'day',i3,'ended')
       read = 0.0

  1000 continue
       prt = 0.0
  2000 continue
       if(icnt .eq. 0)goto 525
       if(hour .ge. 20.0)goto 528
       if(min .ne. 0 .or. irnd .gt. 1)goto 110

       if (id .eq. 0 and irnd .eq. 1)then
           goto 520
       else
           goto 526
       endif

   520 continue
       par1 = par2
       dbt1 = dbt2
       dpt1 = dpt2
   525 read(8,*)par2,dbt2,dpt2
       continue
       i = id/60
       par = ((par2 - par1)/4.)*i + par1
       par = par - 20.0
       rn = (par/4.57)
       dbt = ((dbt2 -dbt1)/4.)*i + dbt1
       dbtk = dbt + 273.16
       dpt = ((dpt2 - dpt1)/4.)*I + dpt1
       dptk = dpt + 273.16
       goto 110
   528 continue
       par = 0.1
       dbt = 24.0
       dpt = 18.0
```

```
C     assign estimated leaf temperature
  110 tlest = tl
      tlestk = tlest + 273.16

C     calculate partial pressure of water vapor in the air (Pa)
      eata = (6.1078*exp((17.269*dpt)/(dpt + 273.3)))*100.

C     calculate saturation vapor pressure of water at air temp (Pa)
      esta = (6.1078*exp((17.269*dbt)/(dbt + 237.3)))*100.

C     calculate absolute humidity of the air (g m^-3)
      ahta = ((eata/(r*(dbt + 273.3)))*mwt)

C     calculate air resistance to heat transfer (s m^-1)
      rsah = (1./(6.62*(u/d)**0.5))*1000.

C     calculate boundary layer resistance to water vapor transfer
      rsaw = 0.9 * rsah

C     calculate saturation vapor pressure of water at tlest (Pa)
      estlest = (6.1078*exp((17.269*tlest)/(tlest+237.3)))*100.

C     calculate slope of saturation vapor pressure over temp (Pa °C^-1)
      s = (estlest - esta)/(tlest -dbt)

C     calculate vapor pressure deficit of air (Pa)
      vpd = (esta - eata)

C     begin iteration to solve for tl
      do 300 lf = 1,30

C     calculate latent heat of vaporization
      lam (2500.9 - 2.345*tlest)*1000.

C     calculate psychrometric constant
      gam ((p*cp)/(lam*mwma))

C     equation # 1 from Idso for tl
      gampl = gam*(1. + rslw/rsaw)
      tl = dbt + ((rsaw*rn)/(da*cp))*(gampl/(s+gampl))-(vpd/(s+gampl))

      test = abs((tl -ta)/tl)
      ta = tl
      if (test .le. 1.0e-3)goto 310
  300 continue
  310 continue

C     calculate leaf to air temperature difference
      deltmp = tl - dbt

C     calculate saturation vapor pressure at leaf temp (Pa)
      estl = (6.1078*exp((17.269*tl)/(tl + 237.3)))*100.
```

```
C       calculate absolute humidity at leaf temp
        ahtl = ((estl/(r*(tl + 273.16)))*mwt)

C       calculate absolute humidity difference
        ahdf = ahtl - ahta

C       calculate wp for use in stomatal conductance equation
        tothet = 0.0
        if (timet .eq. 0)then
           plw = tplw
           thet = thetai(l,1)
           wp = tlulin(thet)
           goto 82
        else
           do 80 l = 1,lay
              tothet = thetac(l,1) + tothet
        endif
           thetf = tothet/lay
        if (thetf .le. wpt)then
           cap = thetf + (fc - wpt)*rc
        else
           expw = totr*delt
           plw = plw - expw
           rplw = plw/tplw
           cap = thetf + (fc - wp)*rc*rplw
        continue
        wp = tlulin(cap,1l)
    82  wp = abs(wp)
        if (rplw .le. 0.25)goto 950
        if (timet .gt. 0) gslw2 = gslw

C       first approach to calculating gslw
C       gamhg = (-0.0005 + (0.073/(ahdf + 6.9446)))/href
C       gamhg = (1./gamhg)*wp/spref
C       gamsp = (103.25 + (wp/(wp*0.00134 + 3.2)))*ahdf/href
C       gamhs = gamhg + gamsp
C       pnot = bet/(rscw - gamhg)
C       gslw = (par + pnot)/((par + pnot)*gamhg + bet)

C       second approach
        gslw = ((par/(213.207 + par)) * (1./(ahdf + 4.9872))) *
               (((0.008 - 0.0006)/((1./ra)*wp + 1.0)) + 0.0006)*rb

        if (gslw .lt. 0.0002)gslw = 0.0002
        gslw = (gslw + gslw2)/2.
        gscm = gslw*100
        rslw = 1./gslw

C       calculate transpiration rate
        tr = (ahdf * gslw)
```

```
C     calculate transpiration rate, mmol basis
      trate = tr * (1000./18.016)

C     calculate total transpiration
      totr = tr * (la/10000.)

CALCULATE WATER FLOW IN THE SOIL
      do 240 l = 1,lay
        do 240 j = 1,kmp
          volwl(l,j) = volw(l,j)
  240 continue

      call integer(timet,delt)
      do 250 l = 1,lay
        do 250 j = 1,kmp
          volw(l,j) = volwn(l,j)
          cond(l,j) = condc(l,j)
          poth(l,j) = poth(l,j)
          theta(l,j) = thetac(l,j)
          flw(l,j) = flwc(l,j)
          flwnt(l,j) = flwnt5(l,j)
  250 continue

C     determine if irrigation is needed
      if (poth(1,1) .lt. wpt .and. irig .eq. 1)then
        goto 330
      else
        goto 275
      endif
  330 continue
      write(6,332)
  332 format(/,'available water in the vicinity of the roots has
    $  been depleted.',/,'how many quadrants do you wish to
    $  irrigate?')
      read(5,*)irkmp
      do 335 l = 1,irkmp
        do 340 j = 1,kmp
          volw5(l,j) = volwi(l,j)
  340    continue
  335 continue
      nirr = irkmp + 1
      do 345 l = nirr, lay
        do 346 j = 1,kmp
          volw5(l,j) = volw(l,j)
  346   continue
  345 continue
      call watflw(timet,volw5,flwnt)

      do 350 l = 1,lay
        do 355 j = 1,kmp
          volw(l,j) = volw5(l,j)
  355   continue
  350 continue
  275 continue

C       calculate the total amount of water in the soil
        tvolw = 0.0
        do 282 l = 1,lay
           do 280 j = 1,kmp
              tvolw = tvolw + volw(l,j)
  280      continue
  282 continue

C       calculate soil resistance to water flow in the
        innermost compartment
        do 290 l = 1,lay
           rssl(l) = csaf(l)/(condc(l,1)*vol(l)*rld(l)
  290 continue

C       calculate potential at root in each soil layer
        do 400 l = 1,lay
           potrt(l) = poth(l,1) -
(flwc(l,1)/((condc(l,1)+rpf)areac(l,1)))
  400 continue

C       calculate shoot xylem potential
        do 665 l = 1,lay
           potlf(l) = poth(l,1) - flwc(l,1)*(rssl(l)+rsrt)/csaf(l)
           tpotlf = tpotlf + potlf(l)
  665 continue
        potxy = tpotlf/lay

C       update counter and time variable
        idd = nint(1./delt)
        if(irnd .lt. idd)then
           timet = timet + delt
           irnd = irnd + 1
        else
           irnd = 1
           ispy = ispy + 1
           timet = ispy*1.0d+00
        endif

        hrcnt = start + (timet/3600)
        hour = hrcnt - (float(iday)*24.0)
        icnt = icnt + 1
        min = mod(ispy,60)
        id = mod(ispy,300)
        if (hour .ge. 30.0)goto 900
        prt = prt + delt
        tend = tf - timet
        smn = 0.0001
        if (prt .ge. pout .or. tend .le. smn)then
           goto 550
        else
            goto 2000
        endif

 PRINT VARIABLES TO OUTPUT FILES
    550 continue
        write(9,640)timet,hrcnt,par,tl,dbt,ahdf,vpd
    640 format(f12.2,f7.2,1z,f7.2,1x,3(f6.2,1x),f8.2)
        write(11,650)hrcnt,(volw(1,j), j=1,kmp)
    650 format(f6.2,2x,6(f10.2,1x))
        write(12,660)hrcnt,(theta(1,j), j=1,kmp)
    660 format(f6.2,2x,6(f.4,2x))
        write(13,670)hrcnt,(poth(1,j), j=1,kmp)
    670 format(f6.2,1x,6(f12.4,1x))
        write(14,680)hrcnt,(cond(1,j), j=1,kmp)
    680 format(f6.2,2x,6(e10.4,1x))
        write(21,651)hrcnt,(volw(4,j), j=1,kmp)
    651 format(f6.2,2x,6(f10.2,1x))
        write(22,661)hrcnt,(theta(4,j), j=1,kmp)
    661 format(f6.2,2x,6(f6.4,2x))
        write(23,671)hrcnt,(poth(4,j), j=1,kmp)
    671 format(f6.2,1x,6(f12.4,1x))
        write24,681)hrcnt,(cond(4,j), j=1,kmp)
    681 format(f6.2,2x,6(e10.4,1x))
        write(15,690)hrcnt,gscm,trate
    690(f6.2,1x,2f12.6)

        if (tend .gt. smn)goto 1000
    950 continue

 CLOSE ALL UNITS
        close(8)
        close(9)
        close(10)
        close(11)
        close(12)
        close(13)
        close(14)
        close(15)
        close(16)
        close(17)
        close(21)
        close(22)
        close(23)
        close(24)
        end
```

SUBROUTINE INTEGR

USES RUNGE-KUTTA FOURTH ORDER FOR INTEGRATION OF NET FLOW RATES

```
      subroutine integr(timet,delt)

      real volwn, volw1, volw22(4,9), volw3(4,9), volw4(4,9)
      real flwnt1(4,9), flwnt2(4,9), flwnt3(4,9), flwnt4(4,9)

      common /amin/ l, j, lay, kmp, kkmp, condc(4,9), pothc(4,9), wpt
      common /amin2/ thetarc(4,9), thetac(4,9), flwc(4,9), flwnt5(4,9)
      common /init/ to, tf, volw1(4,9), volwn(4,9)
      common /soldi/ rld(4), vcc94,9), dr(4,9), areac(4,9), vm, tran

      double precision timet, delt
      call watflw(timet,volw1,flwnt1)

      do 100 l = 1,lay
         do 100 j = 1,kmp
            volw2(l,j) = volw(l,j) + ((delt/2.) * flwnt1(l,j))
  100 continue

      t = timet + delt/2.0
      call watflw(t,volw2,flwnt2)

      do 200 l = 1,lay
         do 200 j=1,kmp
            volw3(l,j) = volw1(l,j) + ((delt/2.0) * flwnt2(l,j))
  200 continue

      call watflw(t,volw3,flwnt3)
      do 300 l = 1,lay
         do 300 j = 1,kmp
            volw4(l,j) = volw1(l,j) + (delt*flwnt3(l,j))
  300 continue

      time = timet + delt
      call watflw(timet,volw4,flwnt4)
      do 400 l = 1,lay
         do 400 j=1,kmp
            volwn(l,j) = volw1(l,j) + ((delt/6.)*(flwnt1(l,j) +
     $      2.*flwnt2(l,j) + 2.*flwnt3(l,j) + flwnt4(l,j)))
  400 continue
C     call del(delt)

  500 return
      end
```

SUBROUTINE WATFLW

CALCULATES VOLUMETRIC WATER CONTENT, WATER POTENTIAL, AND HYDRAULIC CONDUCTIVITY OF THE CYLINDRICAL, CONCENTRIC COMPARTMENTS AROUND THE ROOTS AND WATER FLOW BETWEEN THE COMPARTMENTS

```
        subroutine watflw(timet,volw,flwnt)

        real thetac, vcc, condc, pothc, thetarc, sat
        real resid, vm, vn, satk, alpha, tran, rld, poth(4,9), timet
        real alpt(4,9), alpxp(4,9), flwc, potgd(4,9), poth2(4,9),
        real cond1(4,9), cond2(4,9), totres(4), totcond(4), totfac, dr
        real fac(4,9), flfac(4,9), flwnt(4,9), areac, volw(4,9),
        real res(4,9)

        common /amin/ l, j, lay, kmp, kkmp, condc(4,9), pothc(4,9), wpt
        common /amin2/ thetarc(4,9), thetac(4,9), flwc(4,9), flwnt5(4,9)
        common /soldi/ rld(4), vcc(4,9), dr(4,9), areac(4,9), vm, tran
        common /solparm/ sat, resid, alpha, vn, satk

C       calculate theta, potential, and hyraulic conductivity of the
C       innermost soil compartment
        do 100 l = 1,lay
             thetac(l,1) = volw(l,1)/vcc(l,1)
             if(thetac(l,1) .le. 0)thetac(l,1) = 1.0d-04
           thetst = thetac(l,1)
           poth(l,1) = tlulin(thetst,11)
           pothc(l,1) = -(poht(l,1))
           alpt(l,1) = alpha*poth(l,1)
           alpxp(l,1) = 1. + alpt(l,1)**vn
           condc(l,1) = (satk * (1. - alpt(l,1)**(vn-1.)*alpxp(l,1)
      $                  **(-vm))**2*alpxp(l,1)**(-vm/2.))/3600.
           cond1(l,1) = condc(l,1)
           res(l,1) = 1./condc(l,1)
   100 continue

C       calculate theta, potential and hydraulic conductivity in the
C       outer soil compartments
        do 120 l = 1,lay
           do 120 j = 2,kmp
                thetac(l,j) = volw(l,j)/vcc(l,j)
                if (thetac(l,j) .lt. 0.)thetac(l,j) = 0.0
           thetst = thetac(l,j)
           poth(l,j) = tlulin(thetst,11)
           pothc(l,j) = -(poth(l,j))
           potgd(l,j) = pothc(l,j) - pothc(l,j-1)
           alpt(l,j) = alpha * poth(l,j)
           alpxp(l,j) = 1. + alpt(l,j)**vn
```

```
         condc(l,1) = (satk * (1. - alpt(l,j)**(vn-1.)*alpxp(l,j)
     $                    **(-vm))**2*alpxp(l,j)**(-vm/2.))/3600.
         cond2(l,j) = cond1(l,j-1)
         condc(l,j) = (cond1(l,j) + cond2(l,j))/2.
 120  continue

c     calculate the soil layer conductivity and root length density
c     weighting factor for flow from the first compartment
      do 130 l = 1,lay
         totres(l) = 0.0
 130  continue

      do 145 l = 1,lay
         do 140 j = 1,kmp
            totres(l) = totres(l) + res(l,j)
 140     continue
      totcond(l) = 1./totres(l)
 145  continue
      totfac = 0.0
      do 150 l = 1,lay
         fac(l,1) = rld(l)*totcond(l)
         totfac = totfac + fac(l,1)
 150  continue
      do 160 l= 1,lay
         flfac(l,1) = fac(l,1)/totfac
 160  continue
      do 55 l = 1,lay
         flwc(l,kkmp) = 0.0
  55  continue

c     calculate flow from the first compartment in each layer and then
c     from the outer compartments of each layer
      do 180 l = 1,lay
         flwc(l,1) = tran*flfac(l,1)
      if(timet .eq. 0)flwc(l,1) = 0.0
      if(timet .eq. 0  .or. thetac(l,1) .le. 0)flwc(l,1) = 1.0d-04
      do 180 j = 2,kmp
         flwc(l,j) = ((condc(l,j)*(potgd(l,j)/dr(l,j)))*areac(l,j))
         if(timet .eq. 0)flwc(l,j) = 0.0
         if(timet .eq. 0 .or. thetac(l,j) .le. 0)flwc(l,j) = 1.0d-04
 180  continue

c     calculate the net flow of water into each soil compartment
      do 200 l = 1,lay
         do 201 j = 1,kmp
            flwnt(l,j) = flwc(l,j+1) - flwc(l,j)
 201     continue
 200  continue
 202  continue

      return
      end
```

SUBROUTINE DEL
CALCULATES A VARIABLE TIME STEP

```
      subroutine del(delt)

      real flwc, vcc, dr, thetac, delt
      integer l, j, lay, kmp, il, ij

      common /amin/ l, j, lay, kmp, kkmp, condc(4,9), pohtc(4,9), wpt
      common /amin2/ thetarc(4,9), thetac(4,9), flwc(4,9), flwnt5(4,9)
      common /soldi/ rld(4), vcc(4,9), dr(4,9), areac(4,9), vm, tran

      qmax = 0.0
      il = 1
      ij = 1
      do 100 l = 1,lay
         do 200 j = 1,kmp
            if(flwc(l,j) .eq. 0.0)flwc(l,j) = 1.0
            flwc(l,j) = abs(flwc(l,j))
            qmax = max(qmax,flwc(l,j))
            if (flwc(l,j) .gt. qmax)then
               il = l
               ij = j
            else
               continue
            endif
200     continue
100   continue

      delt = (0.05 * dr(il,ij)) / abs(qmax)
      if (delt .gt. 10.00)delt = 10.0
      return
      end
```

FUNCTION TLULIN

PERFORMS TABLE LOOK-UP AND LINEAR INTERPOLATION ON THE N TABULATED PAIRS OF VALUES X(1)...X(N) AND YX(1)...YX(N).

```
       function tlulin(xval,num)

       dimension ytb(11), xtb(11)
       data ytb /15135., 337.26, 204.4, 153.30, 102.2, 81.76, 61.32
     $           45.99, 30.66, 20.44, 0.0/
       data xtb /0.279, 0.351, 0.371, 0.382, 0.400, 0.412, 0.426,
     $           0.448, 0.467, 0.485, 0.505/

       nm1 = num -1
       do 1 i = 1,nm1
          if (xval .lt. xtb(i+1) .or. i .eq. nm1)goto 2
     1 continue

       perform linear interpolation on ith and (i+1)th enteries
     2 tlulin = ytb(i) + (xval - xtb(i))*((ytb(i+1) - ytb(i))/
     $          (xtb(i+1) - xtb(i)))
       return
       end
```

APPENDIX G

Symbol definitions for Chapter V.

a	minimum stomatal resistance at high radiation from equation (5.4).
AHDF	leaf-to-air absolute humidity difference.
b	coefficient in equation (5.4) determined using nonlinear regression.
c	asymptotic minimum value of leaf conductance as a function of leaf-to-air absolute humidity difference.
C_p	heat capacity of air, J kg^{-1} $°C^{-1}$.
d	leaf width, m.
FAC	plant water storage factor, cm^3 cm^{-3}.
g_s	leaf conductance
$g_{s(max)}$	maximum leaf conductance as a function of soil water potential, determined from data of Stanhill (1978).
$g_{s(min)}$	minimum leaf conductance as a function of soil water potential, determined from data of Stanhill (1978).
G_s	maximum leaf conductance at high light determined from the relationship between leaf conductance and absolute humidity difference.
h	coefficient in equation (5.9) determined using nonlinear regression.
I	photosynthetically active radiation, μmol m^{-2} s^{-1}.
I_o	photosyntheically active radiation parameter required to avoid infinite resistance at zero radiation.
K	unsaturated hydraulic conductivity of the soil, cm s^{-1}.
K_s	saturated hydraulic conductivity of the soil, cm s^{-1}.

K_m	parameter in equation (5.8) determined using nonlinear regression.
m	dimensionless parameter used in Van Genuchten's equation for unsaturated hydraulic conductivity of the soil.
ma	molecular weight of air, g mol^{-1}.
mw	molecular weight of water, $gmol^{-1}$.
n	dimensionless parameter used in Van Genuchten's equation for unsaturated hydraulic conductivity of the soil.
p	parameter used in equation (5.13) set to 300 cm water for simulations on Parkwood, Astatula, and builders' sand.
P	atmospheric pressure, Pa.
q	volumetric water uptake per unit root length, $cm^3\ cm^{-1}$.
r_a	aerodynamic resistance to water vapor transport between the leaf surface and the air, s m^{-1}.
r_s	leaf resistance to water vapor transport, s m^{-1}.
R_n	net radiation, W m^{-2}.
RPLW	relative water content of the plant, $cm^3\ cm^{-3}$.
SP	soil water potential, cm water.
SPREF	reference soil water potential, cm water.
T_l	temperature of the leaf, °C.
T_a	temperature of the air, °C.
TPLW	maximum volumetric water content of the plant, cm^3.
TSLW	soil water content at field capacity, cm^3.
u	velocity of wind, m s^{-1}.
VPD	water vapor pressure deficit of the air, Pa.
WP	effective soil water potential, cm water.

Δ	slope of the saturated vapor pressure-temperature relation, kPa $°C^{-1}$.
γ	psychrometric constant, kPa $°C^{-1}$.
γ^*	$\gamma(1 + r_s/r_a)$.
ψ	soil matric potential, cm water.
λ	latent heat of vaporization, J kg^{-1}.
$\theta_{FC,WPT}$	volumetric water content of the soil at field capacity and wilting point, cm^3 cm^{-3}.

APPENDIX H

TABLE OF SOIL PARAMETERS FOR THREE SOIL TYPES USED IN THE MODEL 'WATFLW'

TYPE	ALPHA	VN	SATK	SAT	RESID	THETAI	FC	WPT
Builders' Sand	0.08778	2.1998	109.0	0.35	0.004	0.047	0.047	0.024
Astatula[†]	0.04214	3.0956	56.5	0.417	0.005	0.088	0.088	0.033
Parkwood[‡]	0.02791	1.49161	1.42	0.505	0.270	0.420	0.420	0.330

[†] Typic Quartzipsammets, uncoated hyperthermic (fine sand).

[‡] Mollic Ochraqualfs, fine-loamy, mixed, hyperthermic (variant fine sandy loam).

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Mary Brakke was born in Marshall, Minnesota. She attended Brimhall Elementary School and Fairview Junior High School in Roseville, Minnesota. After moving with her family to Somerset, Wisconsin in 1971, she attended Somerset High School and graduated in 1975. Foreign languages, English literature and biology were her favorite subjects during high school. In 1977, after finally deciding to go to college, she attended Bethel College, St. Paul, Minnesota for one year. In 1977-1978, Mary lived in Rouen, France and studied French language at the University of Rouen. After returning to the United States she began an undergraduate degree program in Agronomy at the University of Minnesota and graduated in 1982. In July, 1982 she began studying crop physiology in the Agronomy Department at the University of Florida, Gainesville. She received her Master of Science degree in 1984 and will receive her Ph.D. degree in 1989.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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